The influence of bottom-up effects on trophic cascades: a case study of *Orchestia* (Amphipoda) affecting redshank (*Tringa totanus*) predation risk in a saltmarsh ecosystem

by
Nigel Kenworthy

Submitted for the degree of Doctor of Philosophy
to the University of St Andrews

Thesis supervisor:
Professor Will Cresswell
School of Biology
University of St Andrews

January 2018

1. Candidate's declarations:

I, Nigel Kenworthy, hereby certify that this thesis, which is approximately 74,230 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in June 2013 and as a candidate for the degree of Doctor of Philosophy in June 2013; the higher study for which this is a record was carried out in the University of St Andrews between June 2013 and January 2018.

Date January 2018 _____

2. Supervisor's declaration:

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

Date January 2018 _____

3. Permission for publication:

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. I have obtained any third-party copyright permissions that may be required in order to allow such access and migration, or have requested the appropriate embargo below.

The following is an agreed request by candidate and supervisor regarding the publication of this thesis:

PRINTED COPY
a) Embargo on all or part of print copy for a period of 2 years (maximum five) on the following ground(s):

Supporting statement for printed embargo request if greater than 2 years:

Publication would preclude future publication

ELECTRONIC COPY
a) Embargo on all or part of electronic copy for a period of 2 years (maximum five) on the following ground(s):

Supporting statement for electronic embargo request if greater than 2 years:

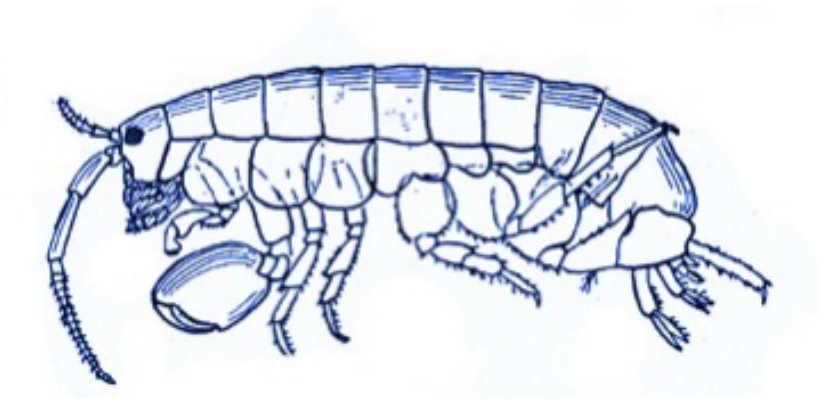
Publication would preclude future publication

ABSTRACT AND TITLE EMBARGOES

a) I agree to the title and abstract being published YES/~~NO~~

Date January 2018 _____ _____
Candidate Supervisor

Orchestia Gammarellus



For my mother, who 47 years ago inspired me with a simple gift –

The Observer's Book of Birds

ABSTRACT

Previous research into bottom-up processes on saltmarshes has mainly focused on the influence of plant succession on herbivores. This study will present original research exploring the influence of bottom-up processes in a saltmarsh ecosystem between three trophic levels: *Orchestia*, redshanks, and sparrowhawks. Density dependence, may be the dominant top-down effect when higher numbers of sparrowhawks and redshanks are present, and may mask top-down and bottom-up trait effects which are constant. Bottom-up effects begin to emerge when cold conditions force redshanks from muddy creeks onto the saltmarsh to forage for *Orchestia*, because their primary prey, *Corophium* become less available. Larger flocks form and feeding on *Orchestia* requires them to balance a need to profit from the best available feeding patches and to be vigilant to sparrowhawk attack. Redshank vulnerability is compounded, because *Orchestia* hide in cold temperatures, so probing in the soil with their heads down makes them more vulnerable to sparrowhawk attack. Larger flocks may be able to exploit areas closer to sparrowhawk-concealing cover at the terrestrial boundary because they feel safer in greater numbers. Warmer temperatures make *Orchestia* more active which attracts redshanks, which can simultaneously feed and be vigilant because they peck and catch crawling and jumping *Orchestia* with their heads up. Consequently, increased flock size may temporarily depress *Orchestia* abundance, so that redshanks become spaced, leaving isolated individuals more vulnerable to attack. Therefore, it is a temperature-dependent bottom-up process which impacts upon both *Orchestia* and redshank behaviour, which then may influence the hunting success of sparrowhawks. Whether the characteristics of this saltmarsh ecosystem and the trophic dynamics can be compared to other examples is questionable. Saltmarshes probably differ in their topography and the way in which environmental conditions affect them that then defines which species are present and how these species interact.

ACKNOWLEDGEMENTS

This research would not have been possible without people who have supported me over the last four years and those who unwittingly inspired me long ago.

I owe the greatest debt to my supervisor Will Cresswell, who came up with an idea and had confidence in me to carry it through. I wouldn't have been able to do this without his encouragement, assistance, advice and most of all his patience.

I'm also grateful to those who kept me going throughout the long journey, and they might be pleasantly surprised that it ended up here. These include Len Barson, Su Engstrand and Dan Harries.

Thanks to the University of St Andrews School of Biology and the NERC who jointly funded this project and to John Anderson who let me use the marvellous photograph on the front cover. The *O. gammarellus* line drawing on page ii is by Stephenson (1928) and was taken from http://www.NOBANIS.org (Accessed: 23 May 2017).

Finally, thanks go to my wife Elaine for her support and understanding. She is someone who I've probably infuriated with my single-minded obsession; she never let it show and of course, she was the driving force.

TABLE OF CONTENTS:

CHAPTER 1. INTRODUCTION: TROPHIC SYSTEMS AND THE FORAGING-PREDATION DYNAMIC

1.1 A general overview of trophic dynamics

This thesis will explore the ways in which the non-lethal effects of predation and the risks of starvation structure ecosystems and what role *Orchestia*, a species of arthropod, plays in this. The research will investigate how *Orchestia* on a saltmarsh in winter on the Scottish east coast influence the distribution and feeding behaviour of redshanks (*Tringa totanus*) and how this affects the trade-off between the twin threats of starvation and predation by a sparrowhawk predator (*Accipiter nisus*). Although top-down effects and their impacts have been well documented in this ecosystem, there is little understanding of the bottom-up role played by *Orchestia*, not only how they determine redshank behaviour, but how this then affects interactions between redshanks and sparrowhawks. Nevertheless, first it is necessary to understand how and why animals make feeding decisions.

1.1.1 Optimal foraging theory

The first research of optimal foraging evaluated theoretical cost benefits analysis for foraging behaviour and was conducted by Emlen (1966) and MacArthur and Pianka (1966). It aimed to form mathematical models from ecological observations of feeding in the field (Krebs *et al*., 1983). Optimal foraging theory considers the general principles that animals use to feed, consisting of four basic categories: (1) which foraging area to visit; (2) time to be spent there; (3) what to eat; (4) the best searching/feeding technique to be used (Pyke *et al*., 1977). Various predictions can then be made so that: (1) predators should prefer prey that results in a higher energetic benefit; (2) they should be selective in choosing their prey; (3) they should disregard other prey however abundant (Pyke *et al*., 1977). An example of optimal foraging theory is given by Irons *et al*., (1986). Foraging by glaucous-winged gulls (*Larus glaucescens*) was greatest at low neap tide, when barnacles (*Balanus glandula*) and mussels (*Mytilus edulis*) were taken, however these species were ignored at low spring tide when sea urchins (*Strongylocentrotus polyacanthus*), black Katy chitons (*Katharina tunicata*) and limpets *Lottia pelta* and *L. scutum* were eaten exclusively. The gulls also selected larger individuals of each prey type. Whereas sea urchins were the preferred prey, during subsequent experiments, equal amounts of each prey species were made available resulting in chitons being eaten more than any other species. It was suggested that the reason for this was that chitons were distributed loosely across the terrain during the experiment, but normally they are less frequent and adhere tightly to the substratum, leading to longer searching and processing time for the gulls. Feeding on chitons in the experiment thus provided the gulls with an increased net energy benefit which they could not get during natural foraging. Therefore, the first two predictions of optimal foraging theory were demonstrated: (1) foraging areas and prey were chosen that maximised net energy gain; (2) gulls fed more selectively on high energy prey. However, to fully understand interactions in an ecological community, other factors need to be considered that relate not only to foraging, but to mortality and the threat of predation to foragers (see 1.1.5). Therefore, an animal must be able to detect patches where food is abundant and of good quality, but sensory capabilities might limit this (Gray and Kennedy, 1994; Tyler and Clapp, 1995; Spaethe *et al*., 2001). For instance, farmland birds preferentially select shorter vegetation when foraging, because taller vegetation hampers prey detectability due to birds using visual cues to detect food (Butler and Gillings, 2004), and because taller vegetation restricts their movement whilst

foraging (Whittingham and Evans, 2004). Likewise, Whittingham and Evans (2004) found that for 11 of 20 species of farmland bird, feeding efficiency was enhanced in shorter vegetation. Detectability of prey was also given as a reason for lapwings (*Vanellus vanellus*) foraging in shorter grass (Butler and Gillings, 2004). In addition, if predators such as waders use visual cues to search for prey, detectability may be dependent upon the level of prey activity, which can be depressed by too many birds foraging in an area, an example being benthic invertebrates withdrawing into their burrows in sediment and mud as waders move over an area (van de Kam *et al*., 2004). Prey detection of ragworm (*Hediste diversicolor*) in mud by dunlin (*Calidris alpina*) was investigated by Santos *et al.* (2009). They discovered that there was poor perception of increased worm presence as dunlin walked across the densest areas and the smaller the area the less likely that they would discover worms. They searched visually until a prey item was discovered and then changed technique to tactile probing. Therefore, there are constraints for dunlin in exploiting the best patches, which can have repercussions for reaching optimal levels of energetic intake (Santos *et al.*, 2009). The problems that redshanks face in searching for *Orchestia* is something that will later be seen to be particularly relevant in this research.

1.1.2 Trophic dynamics: top-down and bottom-up interactions

A fundamental topic in ecology is the dynamics of predator-prey interactions, which impact upon populations and structure ecosystems (Lima, 1998a). A top-down effect occurs when an increase/decrease in the biomass of a higher trophic level (*e.g.* increased population recruitment or alternatively a reduction in that population) results in a decline/increase in the population of a lower trophic level, through the direct or indirect effects of predation (Leroux and Loreau, 2015). Contrastingly, a bottom-up effect is due to an increase/decrease in the biomass in a lower trophic level (*e.g.* fluctuation in the nutrient supply to a primary producer) which leads to an increase/decrease in the population of a higher trophic level. In effect, a top-down effect regulates, whilst a bottom-up effect is limiting (Leroux and Loreau, 2015).

1.1.3 Top-down interactions

Density-mediated versus trait–mediated interactions

Not only do top-down predators reduce prey numbers by direct consumption, otherwise known as density-mediated interactions (DMIs), they must also change the behaviour of prey populations through intimidation which can lead to the prey species investing in energetically costly defensive strategies, in lower fecundity, cause a susceptibility to predation from other species, and trigger emigration from an area. These induced behaviours are known as trait-mediated interactions (TMIs) (Preisser *et al*., 2005), but have also been termed behaviourally-mediated interactions (BMIs) by some authors including Brönmark and Hansson (2007) and De Mars *et al.* (2016). In this instance, trait is a behavioural response by a prey that is plastic and controlled by biotic factors (*e.g.* predator attack rate, life history and metabolic rate) and abiotic factors (*e.g.* weather conditions, elevation and high tide height) (Ohgushi *et al*., 2013). Until fairly recently TMIs have been given scant attention in predator-prey interactions, but are now recognised as being as important, if not more important than DMIs; contributing to 85% of the predator effect particularly in aquatic systems (Preisser *et al*., 2005). Thus, rather than a predator reducing the density of a population directly by killing prey and eating it, a non-lethal predation effect is a compensatory behavioural change in the prey species that is triggered by the predation threat (Cresswell, 2008).

An example of a DMI is given by Lubchenko (1978), where green crabs (*Carcinus maenas*) predate herbivorous snail (*Littorina littorea*), reducing its biomass on the rocky shore. An example of a TMI in an aquatic system is given by Werner *et al.* (1983), where in the absence of largemouth bass (*Micropterus salmoides*), its prey, juvenile sunfish (*Lepomis* spp.), inhabit the pelagic zone. However, if bass are present the sunfish switch habitats into the littoral zone where they hide in denser vegetation and feed on benthic macroinvertebrates (pumpkinseed – *Lepomis gibbosus*).

This risk of being predated has been termed 'the landscape of fear' (Laundré *et al*., 2001) where the fear of being killed not only results in behavioural changes of the prey, but may also alter its physiology and life history (Lima and Dill, 1990). Recent research by Gallagher *et al*. (2017) suggest that this inherent fear amongst prey may have consequences for the way that animals use space and how they are distributed in that space. As an example, they cite previous research by Creel and Creel (1995), Estes and Goddard (1967) and Hayward *et al*. (2006) into African wild dogs (*lycaon pictus*). There is a dietary overlap between the dogs and other predators including lions (*Panther leo*) and spotted hyenas (*Crocuta crocuta*). Catching ungulate prey is energetically costly for dogs, and kleptoparasitism of lion kills by dogs is risky due to threat of being predated by lions. In addition, dog kills are commonly kleptoparisitised by hyenas. At an ecosystem level, where lion and hyena densities are high, dog densities are low and they also avoid areas common to lions (Creel and Creel, 1995). In a similar example Shepard *et al*. (2016) found that herring gulls (*L. argentatus*) use the lift provided by onshore winds to glide instead of flapping their wings, which is energetically costly. This lift is greatest when the wind hits seafront hotels, but the gulls do not take advantage of the best lift here because of the heightened collision risk. They instead inhabit intermediate areas of lift a few meters away (Shepard *et al*., 2016). These two examples demonstrate that animal movement and distribution is not only regulated by the need to take in energy, and the fear of being killed by predators, but by much subtler mechanistic relationships between species and their environment resulting in a more complex series of decisions (Gallagher *et al*., 2017).

In other recent research by Sheriff *et al.* (2015), a TMI was shown to affect a previously studied system involving interactions between snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) as detailed by Krebs *et al.* (2001). This initial study aimed to answer the question, w*hat drives the 10-year cycle of snowshoe hares?* In the system, there are continual oscillations in abundance between the prey, snowshoe hares, and its Canadian lynx predator, and although synchronous, lynx peak abundance lags that of the hare (Krebs *et al*., 2001). Therefore, although a DMI was the principal driver of cyclical snowshoe hare population decrease, Sheriff *et al*. (2015) discovered that the cycles vary in their length, and during a rapid decline in snowshoe hare numbers when predation threat is greater, any surviving fecund females suffer what is described as a 'predator-induced stress', which reduces their subsequent reproductive output and alters the phenotype of offspring. This is despite a reduction in lynx numbers (and predation threat) that is synchronous with that of the hares during the following low phase of the cycle, and even though there is a plentiful supply of food for hares. This indicates a situation where an increased severity of the risk of being killed alters a prey's physiology, in addition to generational changes for the population (Sheriff *et al.,* 2015).

Density-mediated indirect versus trait-mediated indirect interactions

An indirect effect can be added to a DMI/TMI. Hence, a predator affects the density and/or behaviour of a prey species which cascades down to impact the prey's resource. This can be a density-mediated indirect interaction (DMII), where the predator kills prey and reduces its population size, which then impacts upon species in the trophic level below and/or across the community (Sih *et al.*, 1985; Leibold, 1989; Schoener, 1989; Spiller and Schoener, 1990; Jenkins *et al.*, 1992; Paine, 1992; Wootton, 1992; Menge *et al.*, 1994; Schmitz, 1994; De Reuter *et al.*, 1995; Menge, 1995; Křivan and Schmitz, 2004; Ripple and Beschta, 2008; Schmitz, 2008; Colen *et al.*, 2015; Wada *et al.*, 2015; Rinehart *et al.*, 2017), or a trait-mediated indirect interaction (TMII), where prey behaviour is altered by the predation threat, which also cascades down to other trophic levels, and might cause death due to starvation (Abrams, 1984; Mangel and Clark, 1986; Lima and Dill, 1990; Hik, 1995; Dahlgren *et al.*, 2009; Trussell and Schmitz, 2012; Graven and Morgan, 2016), or change life history responses and habitat choice (Sih, 1987; Dobson and Havel, 1988; Crowl and Covich, 1990; Huang and Sih, 1991; Ludwig and Rowe, 1990; Werner, 1991; Werner and Peacor, 2003; Peacor, 2008; Ellrich, 2010; Mowles *et al.*, 2011; Alexander *et al.*, 2013; Freeman, 2017). A TMII has also been termed a behaviourally-mediated trophic cascade (Schmitz *et al.*, 1997), or just a trophic cascade, first described in an experiment by Beckerman *et al.* (1997) in a northeast Connecticut field system, who disabled the mouthparts of spiders to prevent them from killing grasshopper species, but nevertheless found that grasshoppers changed their behaviour by altering activity periods and food selection. Reviews of DMIIs and TMIIs have been undertaken by Werner and Peacor (2003, 2004), Schmitz *et al.* (2004), and Creel and Christianson (2008) who found that behaviour change by prey can occur even when the threat of being killed is minimal.

Lubchenko's DMI crab-snail-algae example above goes on to produce a DMII. Thus, the snail population decreases which allows its food, mainly algae *Ulva intestinalis* and *U. lactuca*, to be released from grazing pressure. The biomass of these species grows and results in them outcompeting tougher less edible algae such as *Chondrus chrispus* and *Fucus vesiculosus*. *Ulva* species take over and dominate the algal community of the shore (Lubchenko, 1978). Moreover, Trussell *et al.* (2004) found in the same ecosystem that snails perceived the predation threat from crabs to be so high that they emigrated out of tidal pools to escape (behavioural change), which again led to *Ulva* becoming dominant. This is an example of a TMII, where the behaviour of prey to predation risk impacts on the species in a lower trophic level, changing the ecological structure of the habitat. In addition, it was discovered that direct predation (DMIIs) had less of an impact than non-lethal predation (TMIIs) when both acted simultaneously in the community dynamics of this system (Trussell *et al.*, 2004), which had previously been noted for ecological communities in general by Peacor and Werner (1997). Likewise, Werner's sunfish-bass research (Werner *et al.*, 1983) was further developed by Mittelbach (1988) who found that the TMI was in fact a TMII because upon changing habitat to the littoral zone, larger pumpkinseed fish are preferentially selected by sunfish as prey, reducing the mean size of the population (Mittelbach, 1988).

1.1.4 Bottom-up interactions

It is suggested that bottom-up interactions can also have a marked influence on ecosystems (Werner and Peacor, 2003). For instance, primary production may be limited by a lack of nutrients and water, which then impacts at a

higher trophic level by restricting the energy intake of consumers (Hunter and Price, 1992; Meserve *et al.*, 2003). An adaptation of this is given by Oksanen *et al.* (1981), who indicated that there is a minimum threshold of productivity that can sustain higher trophic levels, but if productivity increases above this level, the relationship between consumers and their resource changes. This is known as the *exploitation ecosystems hypothesis* (Oksanen *et al.*, 1981; De Angelis, 1992), where if productivity is high, herbivore density may settle to an equilibrium, because it is controlled by carnivore predation. Nevertheless, the resource may continue to grow despite a large proportion being removed by herbivores. A situation might then arise where resource productivity is high and consumer activity is reduced because herbivores are foraging less, which results in decreased availability to a predator (Oksanen and Oksanen, 2000). However, only two trophic levels will exist if resource productivity is low because a small herbivore population is too small to support predators, and if productivity is very low only the resource will be present (Morris, 2008). The fundamental principle about the hypothesis is that each trophic level is regarded as a single entity, even if many species coexist at that level (Morris, 2008). This bottom-up control indicates a TMII working in an opposite direction (to a top-down TMII), because a predator is being affected by a producer via the behaviour of the consumer at an intermediate trophic level (Werner and Peacor, 2003). Likewise, if resource productivity is decreased and energy to the intermediate level depleted, the consumer may take greater risks to obtain food, and increase activity (*i.e.* forage more), which makes it more vulnerable to predation (McNamara and Houston, 1987; Lima, 1998; Werner and Peacor, 2003). Anholt and Werner (1995) conducted experiments to illustrate this and found that when the density of a resource, anuran larvae, was artificially reduced, its odonate predator increased its predation rate by 1.6-fold, even though there was less prey available. This is termed the *predation-sensitive food hypothesis* (Sinclair and Arcese, 1995), which was based on early work conducted by Sih (1980, 1982), Abrams (1982, 1984, 1991), and McNamara and Houston (1987). A bottom-up effect has also been found in marine wrack communities, where the importance of invertebrates that feed on stranded wrack (mainly macroalgal and seagrass deposits), impacted on two species of predator; black-bellied plover (*Pluvalis squatarola*) and western snowy plover (*Chardarius alexandrines nivosus*). When wrack was thinned from some beaches, compared to control beaches where it was left in situ, invertebrates were fewer, as was plover abundance (Dugan *et al*., 2003).

A bottom-up effect might not be triggered simply by biomass fluctuation of the primary producer. In the snowshoe hare/lynx study by Krebs *et al*. (2001) as detailed above, although primarily seen as a top-down system, overgrazing by hares at the peak of their cycle may reduce the preferred winter vegetation resource, but does not trigger direct mortality (starvation accounted for only 3% of deaths in the study), rather it is the reliance upon secondary vegetation such as shrubs and small trees, upon which hares graze, and which produce increased quantities of chemicals (tannins and resins), that reduces their intake and inhibits digestion (Bryant *et al.*, 1985; Krebs *et al.*, 2001). Hares then lose condition, are prone to disease, parasites and increased stress, and their ability to avoid predators is compromised, resulting in a population decline that then also triggers a reduction in lynx numbers (Krebs *et al*., 2001).

Another instructive example of a bottom-up TMII in a marine ecosystem is given by Frederiksen *et al.* (2006) and involves a species in an intermediate trophic level, the lesser sandeel (*Ammodytes marinus*). The study analysed breeding bird surveys in the Firth of Forth, Scotland in conjunction with results from the Continuous Recorder

Plankton survey. Sandeel numbers may be controlled by top-down effects (natural consumption by predators and commercial fishing - DMI), or bottom-up (plankton whose biomass is regulated by climatic variation). Larval sandeel abundance increased 2 to 3-fold in association with an increase of phytoplankton. This impacted on the breeding productivity of four species of seabird that preyed primarily on sandeels to feed their offspring. Therefore, in this example it was abiotic climate-driven variation between years which was the dynamic that drove the system from the bottom-up, in addition to direct top-down influences (Frederiksen *et al*., 2006). What this research showed was a DMI occurring simultaneously with a TMII (driven by an abiotic influence) in the same system. Such complexities arise in almost all systems involving trophic dynamics and any individual system may have idiosyncratic characteristics arising because of the interactions between DMIs and TMIs across a suite of predators and prey.

1.1.5 Recent research of trophic dynamics

Some of the latest research has focused on other cascade effects in food webs. Lyly *et al*. (2105) investigated intraguild relationships between predators and the impact of a top predator, the golden eagle (*Aquila chrysaetos*) on mammalian mesopredators, fox (*Vulpes vulpes*) and pine marten (*Martes martes*). They hypothesised that pine martens in particular would avoid eagle territories due to the predation risk from eagles. Although this was proved in high density eagle territories, low and intermediate eagle densities showed an increase in pine martens, probably because the two species have similar habitat preferences. Foxes increased closer to eagle nests which suggested that the threat of predation by eagles was low and might also be due to both preferring similar prey. In this case, no survival benefits were established for herbivores at the lower trophic level. In contrast, Grason and Buhle (2016) found that an invasive intraguild predator, whelk (*Ocenebra inornata*), consumed 80% of rare native oysters (*Ostrea lurida*) in research conducted on the coast of Washington State, USA. The assumption that the oysters' native predators, various cancrid crabs, were responsible for a serious reduction in oyster numbers was unfounded. Crabs were more likely to consume whelks, but there was no evidence of intimidation by crabs forcing whelks to alter their behaviour to mitigate the risk of predation (TMI). What this research did show was the change in dynamics of an invaded food web and the detrimental effect on a prey resource, in this case the oyster, whose conservation is of concern. A cascading effect was also seen in an upland habitat in Glen Finglas, Scotland, where biodiversity loss occurred due to long-term domestic herbivore grazing, which had multiple effects on the ecosystem (Evans *et al*. 2015). Here, grazing resulted in lower plant biomass and reduced the number of vegetation species leading to fewer arthropods, which led to a reduction in the magnitude of field vole cycles (*Microtus agrestis*). Fewer arthropods negatively impacted both upon ground nesting meadow pipit (*Anthus pratensis*) breeding territories, and reduced vole numbers which affected the food supply for red foxes. In other words, this example illustrated top-down consumption by an herbivore on vegetation (DMI), which produced bottom-up effects impacting on numbers of a species of bird and a small mammal (bottom-up TMI), that altered the predation activity of a top predator (bottom-up TMII) (Evans *et al*. 2015).

The role of detritus and its importance in food webs was recognised by Moore (2004) and has been found to be an integral and widely utilised resource in ecosystems (Leroux and Loreau, 2008). Later research by Wilson and Wolkovich (2011) found that there was an underestimation of scavenging by as much as 16-fold and that energy transfer between trophic levels due to scavenging was greater than that of direct predation. Recent research has

also investigated the role of kleptoparasites and scavengers in trophic dynamics. Kleptoparisitism in food webs was recently investigated by Materassi *et al*. (2016). They took information from several studies and formulated theoretical models to explain the effect that kleptoparasitism has on ecosystems. They found that in guilds of predators, top predators such as large cats, are often kleptoparisitised by omnivorous mesopredators (*e.g*. hyenas), but these top predators can also kill juvenile mesopredators. Although herbivores and the omnivorous mesopredators compete for the same vegetation resource, herbivores are much more adept at exploiting it and are safe from predation by mesopredators which are not able to kill them directly. The top predator can modify its target prey depending on whether juvenile mesopredators or herbivores are more abundant. This prey choice regulates the food web, so that if the top predator consumes herbivores to the exclusion of mesopredators, the whole system fails and both predators and mesopredators become extinct, thereby collapsing the ecosystem to just two trophic levels: resource and consumer (Materassi *et al*., 2016).

Rosenblatt *et al*. (2016) suggested that climate change may also impact upon plant physiology, the timing of seasonal growth, and growth mass, because plant nutrients are controlled by environmental factors including CO_2, temperature, and the availability of water, which are all linked to a warming climate. Therefore, they suggest that there is a linkage to consumers which will be forced to change their feeding methodology and physiology in order to adapt to changes in their food resource. Trophic webs which have thus far appeared relatively simple may in fact be more complex due to changing environmental factors.

Until recently, a reductionist view aimed to simplify predator-prey interactions, presenting theoretical examples that can be applied more generally. Pettorelli *et al*. (2015), however, suggest that character differences in individuals of both prey and predator may also influence their interactions. They suggest that heterogeneity has been overlooked and that variability between individuals needs to be considered if we are to fully understand predators-prey relationships. One example of this might be differences in predation risk of various prey cohorts where data of age-related mortality by predation needs to be collated to produce more accurate theoretical models. Segregation and exclusion of juvenile redshanks from adult feeding areas and the associated increased predation risk is related to this and is further explained in 1.2.1, page 15. Theoretical research by Terry *et al*. (In press) maintains that predator-prey relationships are often influenced by the behaviour of another species in the community and because it is a non-trophic relationship, little weight is given to this. Therefore, if predator-prey relationships are to be researched accurately, the influence of modifying species should be also assessed.

1.1.6 The starvation-predation risk trade-off

With this emergent complexity of top down and bottom up control, unifying principles are needed. One such idea is that DMIs and TMIs arise in all cases because of the starvation-predation risk trade-off: how organisms integrate availability of energy (bottom up) with avoiding (or not) predation from the trophic level above (top down). Hence the behaviour of an animal will be regulated between the two extremes of maximum energetic intake and total avoidance of predation, with the optimal behaviour occurring somewhere between (Lima and Dill, 1990). Therefore, it is suggested that there are foraging-predation risk trade-offs (henceforth the starvation-predation risk trade-off) at intermediate trophic levels, where the emphasis switches between starvation risk and predation risk based on the most immediate threat (Paine, 1980; Carpenter *et al*., 1985). This is because searching

for food requires an animal to move around and by doing this it is more susceptible to being discovered by a predator, therefore, a trade-off needs to balance a sufficient rate of growth with the required level of activity to feed (Abrams, 1991). Trade-offs can result in positive and negative effects for predator and prey which range in magnitude (Schmitz *et al*., 2004). A trade-off might result in a herbivore altering its behaviour by increasing vigilance at the expense of foraging when a predator is present (Abrams, 1984), or switching from an energy-rich habitat to one that is of poorer quality, but offers greater protection from predation (Schmitz *et al*., 2004). Therefore, although an immediate predation risk may be moderated, the consequences could be slower growth and decreased reproductive success (Lima and Dill, 1990; Lima, 1998b). Cresswell (2008) looked at non-lethal effects of predation in birds and indicated that trade-offs should be measured in terms of costs and benefits, such as survival potential and reproductive success, or via alternative factors such as food intake and body weight. Werner and Anholt (1993) suggested prey activity is regulated by the presence of predators and that active species will be more abundant in habitats that have fewer predators compared to a dormant species which inhabits areas where predator numbers are higher. Research by Woodward (1983) showed that different tadpole species (Anura) occur in distinct zones across the permanent to temporary habitat gradient, and that permanent habitats contain greater numbers of predators. In temporary habitats tadpoles are more active, compete better, but are much more vulnerable to predation, whereas in permanent habitats they are less active and vulnerability to predation is decreased (Woodward, 1982).

Lima and Dill (1990) suggest that feeding animals assess their behaviour in conjunction with various components associated with predation risk, such as escaping predator attacks, social interactions with conspecifics, or reproduction success, and that this can be modified accordingly over an organism's lifetime; for example, by the minute or according to season. In effect, all decision-making by prey is adaptive and influenced by predation or other requirements (Lima and Dill, 1990). Life history traits are also affected by trade-offs and there are examples where prey restrict growth to foil predators (Werner, 1992). An example is given by Dodson and Havel (1988) where a freshwater flea (*Daphnia pulex*), in the presence of an invertebrate predator, the grouse-winged backswimmer (*Notonecta undulata*), restricts its egg size, which then reduces the size of subsequent instars by 3.7%. It is suggested that smaller body size somehow reduces the risk of predation and hence mortality (Dodson and Havel, 1988). Similarly, another life history trade-off is shown by the snail *Physella virgata virgata* which responds to cues released into the water by conspecifics that are being eaten by a predator crayfish, *Orconectes virilis* (Crowl and Covich, 1990). In the presence of the crayfish, snails grow larger in a shorter time and are able to reproduce quicker and maintain the population, that was previously reduced by predation (Crowl and Covich, 1990).

Lima (1986) indicates that food availability has a knock-on effect on the starvation-predation trade-off for birds. Areas of higher profitability mean that a bird can increase fat reserves so that it can stave off periods of starvation when prey is scarce, however, a bird benefits from being lean because it spends less time feeding and may be more agile when escaping an attacking predator. Therefore, Lima (1986) produced a simulation experiment that suggested birds should be: (1) fatter in cold and stormy weather when food was less available but they have to increase feeding, (2) thinner if they are under increased predation threat, (3) thinner when temperatures are higher and the starvation threat is reduced, but (4) fatter when food availability and abundance is decreased. Hence,

birds have to regulate optimal levels of fat reserves to reduce mortality, and so that starvation and predation cannot be considered purely in isolation (McNamara and Houston, 1987). Habitats that have the highest food availability for a foraging species may also be the most heavily predated, and safety from predation has to be taken into account when selecting foraging areas (Heithus and Dill, 2002). Foraging animals may be distributed in a habitat correlative to the amount of food available, as was discovered with guppies (*Poecilia reticulate*) (Abrahams and Dill, 1989) and armoured catfish (*Ancistrus spinosus*) (Oksanen *et al*., 1995). Nevertheless, animals may not necessarily forage in the most profitable habitats, but in habitats that are safer but less profitable (Heithus and Dill, 2002). This has been shown empirically by: Holomuzki (1986) for juvenile tiger salamanders (*Ambystoma tigrinum*); Heads (1986) for damselfly larvae (*Ischnura elegans*); Gilliam and Fraser (1987) for creek chub (*Semotilus atromaculatus*); Abrahams and Dill (1989) for guppies; Grand and Dill (1997) for coho salmon (*Oncorhynchus kisutch*); and Vijayan *et al*. (2012) for chital deer (*Axis axis*). The availability of alternative prey may also impact upon the distribution of species which avoid areas where a predator captures and kills this prey and where that species is under threat from the same predator. This was shown for bottlenose dolphins (*Tursiops aduncus*) and tiger sharks (*Galeocerdo cuvier*) in Shark Bay, Australia (Heithus and Dill, 2002). The sharks' primary prey was other species rather than dolphins that occurred in shallow water, and although dolphins preferred to also hunt here, their safety was compromised by reduced echolocation efficiency and extensive seagrass beds which camouflaged the sharks. The riskiness of shallow water meant that dolphins moved to deeper, safer waters to rest. This indicates the importance of considering community structures in conjunction with food availability rather than single species in isolation (Heithus and Dill, 2002).

Switching to alternative prey species may alleviate the risks of starvation (Goss-Custard 1977b). Goss-Custard (1977b) found at various estuaries in southern England, although redshank density and their preferred prey (*Corophium*) density were correlated in one estuary, in another they were not correlated because birds were switching to an alternative food source (*Nereis diversicolor*). Thereby, redshanks were possibly modifying their diet so that they did not have to feed in alternative, riskier habitats. Cresswell (2008) suggested that birds, which are relatively large, mobile and behaviourally well developed, can avoid predation by moving to safer areas, which results in predators having to seek alternative prey species. Similarly, sandpipers were found to avoid landing in some areas during migration, where peregrines (*Falco peregrinus*) were present (Lank *et al*., 2003). Lima (1998a) states that whole ecosystems may be impacted where one prey type changes its behaviour to avoid a predator which then switches to alternative prey, causing cascading trophic effects across the system, as has been already described above as part of the consequences of trait-mediated interactions. Huang and Sih (1990) describe prey species, the small-mouthed salamander larvae (*Ambystoma texanum*) and freshwater isopod *Lirceus fontinalis*, which although are non-competitive with each other, become so when they are the focus prey of a predator, the green sunfish (*Lepomis cyanellus*). Presence of sunfish decreased isopod activity outside their shelters, and as male isopods were more active than females they were predated more, however, salamander larvae in the same shelters ousted isopods so that females also suffered predation. Active isopods outside shelters also caused sunfish to become more active which produced an anti-predatory behavioural change in salamander larvae that decreased their time outside shelters (Huang and Sih, 1990). Consequently, activity levels of one species can impact upon the predation of another by a shared predator.

Trade-offs can also be observed where species view proximity to cover as either a threat, or a safe refuge, therefore, time spent on vigilance and foraging is dependent on how they evaluate whether predation or starvation is the greatest risk at that moment (Inger *et al.*, 2006; Watson *et al.*, 2007). Such habitat selection was demonstrated to be important for white-throated sparrows (*Zonotrichia albicollis*) by Schneider (1984). Here, the starvation-predation risk trade-off was measured by putting equal quantities of food at increasing distances from cover. Sparrows considered that feeding closer to cover was safer from predation and they would exhaust food supplies here before moving further away. Furthermore, dominant birds fed closer to cover, whereas subordinates were forced to feed at greater distances. This suggests that sparrows lower their predation risk, but at the expense of foraging more efficiently (Schneider, 1984).

Valone and Lima (1987) found that several bird species spent less time handling food in the open, compared to when they were under cover which allowed them to slow down their handling and processing of food items. These birds saw foraging further from cover as a threat, whereas slower eating increased nutritional benefits (Valone and Lima, 1987). Food quality is an important consideration, but it might be the case that maximising energetic intake in the best areas is not compatible with minimizing predation risk (Lima and Dill, 1990). When feeding in the open, grey squirrels (*Sciurus carolinensis*) and black-capped chickadees (*Poecile atricapillus*) were discovered to reject small but high energy food items in the open, in preference for larger lower energy food items which they took to safer areas in cover before processing (Lima and Valone, 1986). This is indicative of the starvation-predation risk trade-off where the time spent foraging is associated with vulnerability to attack by a predator (Lima and Dill, 1990). Likewise, Lima (1988) found that for dark-eyed juncos (*Junco hyemalis*), processing of energetically rich food was undertaken in a head down position which impacted upon vigilance and awareness, compromising their ability to detect predators. They therefore select less profitable food which they can process with the head up, which allows for better predator detection. Additionally, if there is an increased predation threat, they may still be able to eat the more profitable food item if they form larger flocks (Lima, 1988). In contrast, some species such as, yellow-bellied marmot (*Marmota flaviventris*) (Carey, 1985), and several species of African antelope (Underwood, 1982), view cover as dangerous habitat that hides predators and they aim to maximise distances from it. It was also found by Lima (1987) that there are discrepancies in the way that house sparrows (*Passer domesticus*) view distance to cover along with flock size and levels of vigilance. He found that if they were feeding away from cover and if flocks were bigger, birds were less vigilant, even though they preferred to forage in patches closer to cover where they felt safer (Lima, 1987).

A further complexity to the starvation-predation trade-off may involve multiple predators. Most communities have several predators which can lead to interactions between them and affect the dynamics of the community (Siddon and Witman, 2004; Sih *et al.*, 1998). When multiple predators interact, this may result in interference, facilitation, or have no effect and will be dependent upon of their different hunting/foraging strategies (Crowder *et al.*, 1997; Siddon and Witman, 2004; Schmitz, 2007). Therefore, predators may complement each other and their foraging activities may lead to shared benefits including higher intake and increased growth (Soluk, 1993; Soluk and Richardson, 1997; Losey and Denno, 1998; Eklov and van Kooten, 2001); intake success may be reduced if there is intraguild interference or competition between predators (Sih *et al.*, 1998; Siddon and Witman, 2004; Griswold and Lounibos, 2006; Schmitz, 2007); or there may be no effect if the interaction between predator

species is no different to that within the same species (Schmitz, 2007). Anti-predation behavioural change by prey species, which might include switching habitats or feeding less in the open, can have a big influence on all predators of that prey (Matsuda *et al*., 1993; Crowder, *et al*., 1997; Siddon and Witman, 2004; Preisser *et al*., 2007). Van Son and Thiel (2006) examined the predation on prey species (amphipods), on a rocky intertidal shore, by ribbon worms (Nemertea) and shrimp, which are bottom feeders and surprise hunters, and juvenile fish which occur in the water column. Ribbon worms had no effect on the behaviour of amphipods, but shrimps caused them to spend more time in open water, whilst the presence of juvenile fish caused them to remain in refuges. The greatest predation occurred when shrimps and fish were both present and caused a conflict in the amphipod anti-predation strategy, whether amphipods were in open water or refuges (van Son and Thiel, 2006). Therefore, changing habitats did not help them to avoid predation. Similar behaviour can be seen in a two-predator system involving peregrines and sparrowhawks, which both predate redshanks. Peregrines hunt using various behaviours, but most bird prey is taken in flight over open landscapes and water, and rarely along wood boundaries (Dementiev and Gladkov, 1951; Cade, 1960; Voous, 1961; Portenko, 1968; Glutz Von Blotzheimet *et al*., 1971). They also known to take prey from the ground (Witherby *et al*., 1939; Roberts, 1946; Harris and Clement, 1975; Stirling-Aird, 1977). Prey on the ground is struck (Glutz Von Blotzheim *et al*., 1971) and the rear talon hits the back of the neck or head so that the prey is killed immediately; if not, a bite to the neck or head will then kill the prey (Cade, 1960; Baker, 1967). Peregrines use this technique when hunting redshanks in open areas, often when they are feeding in shallow water or mud, where a circling peregrine will make several swoops to try and pick a redshank from the ground. As a defensive mechanism redshanks will flock tighter together, stay in position and sink lower as the peregrine swoops; an observation made at the study site by Cresswell (1993), and at redshank feeding pools near Musselburgh 20 miles to the north (pers. obs.). This contrasts with the anti-predatory behaviour when faced with predation from sparrowhawks, which may stalk prey, swooping and landing at short stops, often in a tree where they can remain hidden (Newton, 1986). A sparrowhawk can then perform a surprise attack and will either catch the redshank on the ground, or a few meters in the air as it tries to escape (Cresswell, 1996). On detection of an attacker, redshanks will take flight as a flock, resulting in three specific outcomes: the target individual is caught; the target is tail-chased by the sparrowhawk; or the chase is ended, usually within 30m (Newton, 1986). These two anti-predation behaviours show that the predation element of the trade-off is complex and is modified, dependent on the predator.

The peregrine/redshank anti-predation behaviour above shows that a proactive behavioural adjustment such as grouping closer together and individuals making themselves a smaller target might mitigate risk, so that an ultimate escape response is not required. Consequently, this may enable prey to remain in profitable feeding areas, in contrast to relocating to other areas which might result in more energy expenditure involved in the transit (Ydenberg and Dill, 1986). Prey also have to assess the distance between them and the predator so as to time their escape initiation so it allows them to reach safety (Lima and Dill, 1990; Quinn and Cresswell, 2005). An example of this is with African cichlid fish (*Melanochromis chipokae*) which occur on rocky sea beds. Individuals further from safety begin their escape sooner when a predator appears, but all fish in the shoal maintain a constant distance to the predator until safety is reached (Dill, 1990). Therefore, flight initiation appears to trade-off the best escape technique with expending the least amount of energy.

By modifying foraging behaviour prey can aim to optimise energetic intake whilst maintaining awareness of the predation risk. However, being vigilant can compromise feeding intake, so there is a benefit to reducing vigilance during periods of lower predation threat (Lima and Dill, 1990). The probability of predator detection can be increased if animals feed in groups (Elgar, 1989), and Pulliam (1973) put forward the hypothesis of a negative correlation between group size and vigilance. Therefore, an increase in the number of individuals in a group should result in a greater probability of an attack being detected (Kenward, 1978; Lima, 1995; Roberts, 1996). Hence, as flocks of great crested terns (*Thalasseus bergii*) get larger, they have been found to scan less frequently (Roberts, 1995) and house sparrows reduce the length of scanning periods in bigger flocks (Studd *et al*., 2011). This has been termed the *many eyes* hypothesis of vigilance behaviour (Bertram, 1978; Kenward, 1978; Lima, 1995). Feeding technique can also be an indication of vigilance level, where an animal searching for food with its head up can detect an attack from a predator quicker compared to when it has its head down (Lima and Bednekoff, 1999). Therefore, vigilance is defined by Whittingham and Evans (2004) as an animal that has its head up for periods during foraging. When studying farmland granivorous birds, Butler and Gillings (2004) decided that chaffinches (*Fringilla coelebs*) were vigilant when their heads were above the level of their backs, but not vigilant when their heads were down searching for seeds and pecking the ground. Cresswell *et al.* (2003) also found an association in chaffinches where increased intake rate led to increased predator detection; birds that pecked quicker in areas of greater food abundance had a quicker head up rate and were better able to detect an attack by a predator. Thus, it was suggested that a scarcity of food not only resulted in lower energetic intake, but a reduction in anti-predation effectiveness (Cresswell *et al.*, 2003). Nevertheless, Cowlishaw *et al.* (2004) found that samango monkeys (*Cercophecus mitis*) when eating flowers and berries, can do so whilst scanning for predators (*i.e.* food handling using hands requires less visual attention), illustrating a modification to the starvation/predation trade-off. Sansom *et al*. (2009) also suggest that when redshanks search for *Orchestia*, the attention required in doing so results in a head down or head-horizontal position which compromises their ability to detect an attack, something which was also discovered for blue tits (*Cyanistes caeruleus*) by Kaby and Lind (2003).

1.1.7 Trophic dynamics on saltmarshes and *Orchestia*

There are several studies of *Orchestia* on saltmarshes including their: presence and distribution (Goodhart, 1941; Wildish, 1970b; 1987; Perkins, 1974; Laverack and Blackler, 1974; Meaney *et al*., 1976; Ingolfsson, 1977; Kneib, 1984; Henzler and Ingolfsson, 2007; Mantzouki *et al.*, 2012; Schrama *et al*., 2012); life history traits (Den Hartog, 1963; Wildish, 1969; Bradley, 1974; Sprung and Machado, 2000; Dias and Sprung, 2004); tolerances to salinity and temperature (Morritt and Spicer, 1998); diet (Creach *et al*., 1997); entrained rhythms (Wildish, 1970a); and as food for redshanks (Goss-Custard and Jones, 1976; Yasue *et al*., 2003; Minderman *et al*., 2006; Cresswell and Whitfield, 2008; Sansom *et al*., 2009), curlew (*Numenius arquata*) (Goss-Custard and Jones, 1976), common sandpiper (*Actitis hypoleucos*) (Arcas, 2001), varied thrush (*Ixoreas naevius*) (Egger, 1979), brown rat (*Rattus norvegicus*) (Drummond, 1960), and during tidal inundation by various species of fish (Laffaille *et al.*, 1998, 2005). As macro-detritivores *Orchestia* are more associated with detritus and the brown food web rather than the green food web based on primary production, although Zou *et al*. (2016) suggest that top-down/bottom-up control of both food chains, once thought of as separate, are linked and have to be considered as part of the same trophic mechanism. Therefore, predation of decomposers can influence the amount of primary production in the green

food web where the result could be a positive or negative effect, dependent on the proportion of nutrients (carbon:nitrogen) produced in the brown food web and released into the system, which may stimulate or retard vegetation growth (Zou *et al*., 2016). Furthermore, it is suggested that there is only a weak effect of detritivores on top predators in the green food web (Arab and Wimp, 2013)

Schrama *et al*. (2012) hypothesise that bioturbation by *O. gammarellus* promotes the growth of sea couch grass (*Elytrigia atherica*), an anoxia-intolerant saltmarsh plant of the late successional stage. This is because the digging by *O. gammarellus* oxidises the top layer of anoxic sediment (Schrama *et al*., 2012). In addition, because *O. gammarellus* comprises ~90% of the faunal biomass of a saltmarsh, it produces a large amount of excrement on the surface and in conjunction with digging, encourages nitrogen mineralisation allowing the plant to flourish. The bottom-up effect is amplified because the tall structure of sea couch grass restricts grazing by herbivores (Schrama *et al*., 2012). However, grazing by large herbivores such as domestic cattle and sheep can have a top-down effect on *O. gammarellus*, where trampling compacts the soil, increases waterlogging and reduces redox potential; a lowering of the oxygen-reduction potential of the soil (Adam, 1993). *O. gammarellus* is averse to these conditions and therefore there is little bioturbation of the soil in these areas, less nutrient recycling and reduced vegetation growth (Schrama *et al*., 2013).

1.1.8 Which is the controlling effect: top-down or bottom-up?

Although the last example indicates that both effects can occur in the same system, the question is which is dominant? Top-down control dictates species of vegetation present in a habitat, competition between those species, besides overall vegetation biomass (Hairston *et al*., 1960), and its effect should increase along with an increase in primary production (Fretwell, 1977; Oksanen *et al*., 1981; De Angelis, 1992). As mentioned previously, low primary production, possibly caused by lack of nutrients and water, will restrict herbivore presence (bottom-up effect), but a top-down effect will occur where there is intermediate primary production and herbivores regulate plant biomass (Kuijper and Barker, 2005). However, plant consumption is reduced at high levels of productivity because the growing herbivore population will be depredated by carnivores (Oksanen and Oksanen, 2000). Nevertheless, it might not always be the case that high primary production biomass results in carnivores regulating increased herbivore abundance, because foraging quality caused by a change in habitat composition and an increase in the carbon:nitrogen ratio might result in fewer herbivore consumers even if carnivores are absent (Kuijper and Barker, 2005). This has been termed the *quality threshold hypothesis* (van de Koppel *et al.*, 1996; Olff *et al.*, 1997; Huisman *et al.*, 1999), and suggests that bottom-up effects are equally important in habitats where primary production is high.

Therefore, two views are held. First, the bottom-up concept is that members of each trophic level are limited by food availability. Second the top-down concept is that the top trophic level is food limited, and at alternate levels below this they are predator and then food supply limited (Bowlby and Roff, 1986). Perhaps a more useful way of understanding the conflicting primacy of top-down/bottom-up effects, and something that will be particularly relevant in this research, was offered by Hunter and Price (1992); the question is, *not which has the greatest effect, but what variables control the limitation of resources and predation*?. The answer will identify temporal and spatial factors that determine whether resources or predators are dominant (Hunter and Price, 1992).

1.2 Trophic dynamics at the study site

1.2.1 Evidence of top-down interactions

Previous research at the study site based at Tyninghame saltmarsh, East Lothian (56˚00'30.15", 2˚35'26.76"W) (Cresswell, 1994a, 1994b; Cresswell and Whitfield, 1994; Hilton, Ruxton and Cresswell, 1999 ; Cresswell and Quinn, 2004; Lind and Cresswell, 2005; Quinn and Cresswell, 2006; Sansom *et al*., 2009; Cresswell, 2010) investigated non-lethal effects from a top-down perspective mainly via interactions between sparrowhawks and redshanks. Even though Bakker *et al*. (2015) indicated that top-down influences are rare on saltmarshes, Cresswell and Whitfield (1994) found that raptors such as merlin (*F. columbarius*), peregrines and sparrowhawks attacked and killed over 50% of the wintering wader population, mostly redshank and dunlin (*Calidris alpina*). The death of wader prey might not be directly the result of raptor predation. Almost one third of wader deaths after a sparrowhawk attack were caused by kleptoparasitism by carrion crows (*Corvus corone*), where crows would dispossess sparrowhawks either on the ground or by forcing them to release prey in flight (Cresswell and Whitfield, 1994). Moreover, at the study site, over 3 consecutive winters between 1989 and 1992, the authors estimated that redshanks on the saltmarsh numbered 260-360, 175-379, and 180-443 birds respectively. Of these, the numbers killed by raptors (and kleptoparasited by carrion crows (*C. corone*) from raptor kills) were 113, 191, and 255 giving a grand total of 559; around 438 of these were killed by sparrowhawks, or kleptoparasited from them (Cresswell and Whitfield, 1994). This is an example of a DMI, where there is a considerable decrease in the numbers of prey caused by density-dependent predation. Likewise, it was found that there was a behavioural response by redshanks which formed larger flock sizes to mitigate the predation threat (TMI) (Cresswell, 1994b). Other early research suggested that sparrowhawks preferred to attack larger flocks, which seemed contradictory because their success rate was less than when smaller flocks were attacked (Cresswell, 1994b). Contrastingly, Cresswell and Quinn (2004) discovered that sparrowhawks were twice as likely to attack the more vulnerable prey group (fewer birds in the flock and when distance to sparrowhawk-concealing cover was decreased), and redshanks were more likely to be killed when they did so. However, flock size and variability in abundance is only a partial explanation as to why sparrowhawks attack redshanks and why redshanks change behaviour to reduce this threat. Quinn and Cresswell (2004) found that sparrowhawks evaluated the success of previous attacks which influenced subsequent attack decisions, and attack probability decreased when wind speed was higher because it was thought that this interfered with a sparrowhawk's flight manoeuvrability and therefore its hunting capability. Similarly, the composition of redshank flocks may change over the winter with more adult birds feeding on the saltmarsh in mid-winter to early spring, which accounted for a rapid decrease in attacks because adults have a greater experience at evading capture (Cresswell, 1994a; Cresswell and Whitfield, 1994), which is also noted in other species such as adult ants which avoid antlion pits (larva of winged sit-and-wait insects – *Myrmelondidae* spp.) (Hollis, 2017), and adult elk whose learned behaviour allows them to better escape predation by wolves compared to juveniles in Yellowstone National Park, Wyoming (Mech *et al*., 2001). Predators may target juvenile prey specifically because they are vulnerable when compared to adults, as in the case of mosquitofish (*Gambusia affinis*) that feed on mosquito larva (Liu and Gourley, 2014) and cylindrical bark beetles (*Aulonium* species) that feed on Asian longhorned beetle larva (*Anoplophora glabrippenis*) (Li *et al*., 2009; Gourley and Lou, 2014). It is suggested by Cresswell and Quinn (2004) that not only do redshanks assess the behaviour of other members of the flock so that they can consider their vulnerability to predation accordingly

(demonstrating a trade-off), but sparrowhawks assess the vulnerability of flocks and identify the best group to attack (although the authors also said that sparrowhawks may occasionally attack opportunistically).

Adults excluding juveniles from safer foraging areas was detailed by (Cresswell, 1994a), where adult redshanks fed on mussel beds to the east of the saltmarsh where sparrowhawk attacks were infrequent, denying access to juveniles, which were then forced to feed on the saltmarsh that had a greater predation risk. Adults recognised the threat of predation which caused them to behave antagonistically toward juveniles, but juveniles benefited from higher energy intake at the expense of being attacked, which also entailed them feeding closer to cover (Cresswell, 1994a). Nevertheless, Hilton, Cresswell and Ruxton (1999) indicated that redshanks on the saltmarsh monitor sparrowhawk activity and change their behaviour on days when there are more attacks, by foraging further from cover. In fact, sparrowhawk attack success showed an exponential decline further from cover, and it was indicated that this threshold was 30m, below which redshanks only forage when temperatures are colder and the starvation risk increases (Cresswell *et al*., 2010). This riskier foraging strategy meant that sparrowhawks are more successful at catching redshanks in colder conditions (Hilton, Ruxton and Cresswell, 1999). Sansom *et al*. (2009) indicated that predator avoidance behaviour should be the primary aim of redshanks feeding on the saltmarsh. However, avoidance whilst simultaneously reaching an optimal energy intake might not always be possible because starvation risk increases in cold weather due to higher energetic demands.

Bird spacing in flocks also influences the nature of sparrowhawk attacks (Quinn and Cresswell, 2006), and behavioural decisions made by redshanks regarding spacing are a direct result of the predation threat. Redshanks that were targeted by sparrowhawks were 35% further away from conspecifics that were not targeted, when distance from the sparrowhawk was accounted for. Moreover, these targeted birds tended to be in the outer margins of the flock reinforcing Hamilton's *selfish herd theory* where individuals in a group aim to maximise their safety by putting conspecifics between themselves and a predator (Hamilton, 1971). Tighter spacing benefits redshanks in two ways, they form tighter groups in dangerous areas when stationary, and when mobile, closer spacing confuses attacking sparrowhawks during flight escape (Quinn and Cresswell, 2006). Therefore, for redshanks, the starvation-predation trade-off produces a mismatch between optimisation of the best feeding technique in the most profitable areas, whilst simultaneously attempting to apply the most suitable anti-predation behaviour (Cresswell and Whitfield, 2008).

1.2.2 Evidence of bottom-up interactions

Orchestia distribution on saltmarshes has been described as patchy (Yasue *et al*., 2003), with some areas being hotspots of increased density and biodiversity (Pavesi and De Mathaeis, 2013). *Orchestia* not only evade predators by hiding in wrack banks (Karlbrink, 1969; Wildish, 1969), but also by hiding in dense vegetation (Kraeuter and Wolf, 1974; Colombini *et al*., 2013) and fissures in the soil (Den Hartog, 1963; Colombini *et al*., 2013), which are numerous close to saltmarsh creek edges. The added advantage of inhabiting these areas is that they provide shelter from drying winds and higher temperatures, and reduce the greatest risk to *Orchestia*: desiccation (Backlund, 1945; Karlbrink, 1969; Wildish, 1970a ; Spicer *et al*., 1987; Jones and Wigham, 1993; Morritt and Ingolfsson, 2000; Sprung and Machado, 2000; Rossano *et al*., 2009). Although not a burrowing species *Orchestia* also hide by digging into the substrate (Persson, 1999; Pavesi and De Mathaeis, 2013) up to a

depth of 10cm (Den Hartog, 1963). Therefore, this avoidance behaviour, in part caused by the threat of predation, may also impact upon the way in which redshanks feed, thus resulting in a bottom-up effect. Minderman *et al.* (2006) were the first to suggest that there may be bottom-up control by *Orchestia* in this ecosystem upon redshanks, although there is little subsequent research to substantiate this. Hence, redshanks switch their prey target to *Orchestia* and although redshank behavioural response to predation risk and interference competition demonstrate a top-down effect, *Orchestia* occurrence, and patchiness of distribution and their hiding behaviour, may limit accessibility of this food resource to redshanks exerting a bottom-up influence (Minderman *et al*., 2006).

Minderman *et al*. (2006) also discovered that hiding behaviour of *Orchestia* may be amplified where their activity becomes depressed in reaction to disturbance by feeding redshanks. In effect, a reduction in surface density is not caused by direct predation. Thus, *Orchestia* escape from the surface into the soil and are less available for a few hours. In *Orchestia* habitat, redshanks had a greater success rate foraging at the front of the flock compared to the rear, and success rate was reduced if more birds passed through a feeding area, suggesting that there was a non-aggressive interference amongst conspecifics, resulting in birds walking quicker and becoming more widely spaced. *Orchestia* therefore produce a bottom-up influence on redshanks where isolated birds are more at risk of attack from sparrowhawks. Moreover, if *Orchestia* become harder to detect, more time and effort will be expended on feeding which will lead to redshanks becoming less vigilant and less able to detect an attacking sparrowhawk (Minderman *et al*., 2006). An added effect was discovered by Cresswell and Whitfield (2008) who found that *Orchestia* were most abundant closer to predator-concealing cover. This along with interference competition (wider spacing), activity depression, and reduced predator vigilance could also result in redshanks becoming more vulnerable to sparrowhawk predation. These behavioural reactions illustrate that a species in a lower trophic level can have an influence on a higher trophic level via an effect on the behaviour of a species at an intermediate level (TMII from the bottom-up) (Cresswell and Whitfield, 2008). This thesis explores this in further detail.

Flocking in redshanks is also most likely a product of *Orchestia* occurrence (bottom-up control) and one would expect larger flocks to occur in *Orchestia* patches and where they are more abundant, which is stated by Goss-Custard and Jones (1976) for redshanks feeding on *Orchestia* and *Corophium* on the Wash, East Anglia, and Yasue, *et al*. (2003) for redshanks feeding on *Orchestia*, *Hydrobia ulvae* and *Littorina* at the study site. Anti-predation benefits arise in larger flocks due to the three tenets of vigilance, dilution and confusion (see 4.1.1) (Hilton, Cresswell and Ruxton, 1999). Nevertheless, the size of the flock may hamper the escape speed of redshanks because there are fewer vigilant individuals in larger flocks, and there is an escape delay because most birds only respond to the threat of sparrowhawk attack by reacting to the flight of conspecifics (Quinn and Cresswell, 2006). Likewise, birds further from their nearest neighbour were the latest to take off (Hilton, Cresswell and Ruxton, 1999). If higher *Orchestia* density leads to larger flock size it is possible that dilution and confusion have a greater mitigating effect upon direct mortality from sparrowhawk predation than vigilance, which appears to be reduced as flock size increases. Moreover, Quinn and Cresswell (2005) also indicated that the response time between detection of a predator and escape by the rest of the flock lengthened in larger flocks although confusion and dilution provided increased benefits. Also, individual spacing was critical for successful escape of non-detecting birds and escape was quicker as flock size increased (Quinn and Cresswell, 2005). Hilton,

Cresswell and Ruxton (1999) also suggest that even a slightly delayed reaction in escape flight launch might influence the probability of a redshank being captured, for instance, where flocks feed closer to predator-concealing cover (redshanks possibly attracted by denser *Orchestia* patches), or flocks are larger. Despite this, later research indicated that sparrowhawk attack success decreased as flock size increased, where there was a sharp decline initially before it levelled off at about 40 birds (Cresswell and Quinn, 2011). Therefore, *Orchestia* occurrence and density may not only produce a bottom-up DMI, but also a bottom-up DMII where sparrowhawk success is indirectly affected by *Orchestia* through the flocking behaviour of redshanks.

1.3 Thesis aims

This thesis will determine the impact of *Orchestia* on a saltmarsh ecosystem with reference to bottom-up effects upon redshanks and how this impacts upon redshank ability to manage the starvation-predation risk trade-off when faced with predation by sparrowhawks. Although an initial aim of the research was then to link this to how redshanks directly managed their risk of predation from sparrowhawks, the rates of direct predation and anti-predation interactions between the two species were found to now be very low, compared to high rates historically (Cresswell and Whitfield, 1994). This is probably because numbers of overwintering redshanks have reduced considerably on the saltmarsh since the early '90s, along with sparrowhawks for which they are a prey target. Therefore, the thesis will concentrate on how the distribution, density and behaviour of *Orchestia*, in response to their own predation risk from redshanks, determine the anti-predation behaviour of redshanks in terms of proxies of predation risk: foraging behaviour on the higher risk saltmarsh, distance to cover and group size.

These general aims are as follows:

1. Because no extensive research has been conducted on *Orchestia* at the study site, the species of *Orchestia* will be verified, the hypothesis being that *O. gammarellus* and *O. mediterranea* will be present. In addition, it is presupposed that the average size of each species as will be different from one another, there will be sexual dimorphism, and the composition of each species' population will be consistent across years of this research as will their occurrence and abundance in specific areas of saltmarsh (Chapter 2).

2. The presence of redshanks on the saltmarsh will be assessed in terms of biotic and abiotic variables because it is predicted that conditions such as weather, tidal coverage, seasonal influence, *Orchestia* density and species and structure of vegetation will affect this (Chapter 3).

3. It is expected that the size of redshank flocks will vary in relation to:
    a. Weather, where redshank flocks will larger in colder and windier weather because they will seek shelter on the saltmarsh.
    b. Distance to cover, because it is considered that larger flocks will occur closer to cover, where they feel safer because larger flocks help mitigate the threat from sparrowhawk predation.
    c. Density of *Orchestia*. It is hypothesised that redshank flocks will be larger in areas of higher *Orchestia* density, because these will be preferred feeding areas.

d. Species and composition of vegetation, because *Orchestia* species will favour types of plant and the plant communities commonly found in their own habitats.

e. Confounding effects of tidal coverage and season, where it is predicted that redshank flocks will be larger in the reduced area of uncovered saltmarsh around the time of high tide, and be larger in January and February when redshank numbers are highest (Chapter 4).

4. Three redshank feeding behaviour traits will be measured including steps, effort and success against biotic and abiotic predictors to determine how, why and where they feed on *Orchestia*. It is hypothesised that redshanks will have an increased:

a. Step rate in sparser vegetation where *Orchestia* density is low and in warmer conditions when *Orchestia* are more mobile and they must chase them.

b. Effort (probing) in colder conditions when redshanks must search in saltmarsh soil for buried *Orchestia*.

c. Swallows in colder conditions when redshanks need a higher daily energy intake to survive (Chapter 4).

5. Finally, an assessment will be made of the relative impacts of density-mediated and trait-mediated effects that influence this saltmarsh ecosystem, specifically the bottom-up influence of *Orchestia* upon redshanks and sparrowhawks (if numbers are sufficient). Moreover, an overall evaluation will be made of factors that regulate these effects and the importance of looking at how parts of the system relate, rather than focusing on one linear trophic structure. Therefore, it is hypothesised that bottom-up effects influence this ecosystem, and the importance of these effects can be quantified (Chapter 5).

CHAPTER 2. *ORCHESTIA* DISTRIBUTION AND BEHAVIOUR

2.1 Introduction

Orchestia anti-predation behaviour influences trophic dynamics via bottom-up control (Minderman *et al*., 2006) because of what Sinclair and Arcese (1995) term the *predation-sensitive food hypothesis*, where interference competition by feeding redshanks depresses *Orchestia* numbers resulting in them becoming temporarily unavailable. This may result in redshanks focusing more on searching for a diminishing resource (*Orchestia*), making them more vulnerable to sparrowhawk attack (Minderman *et al*., 2006; Sansom *et al*., 2009). However, it is hypothesised that *Orchestia* may exert bottom-up control on predator-prey interactions in other ways such as: their distribution and if and how this changes spatially; their means of evading predation by hiding, including escaping behaviour; and their reaction to variation in weather conditions such as temperature and wind speed. Before these mechanisms can be considered in detail it is necessary to understand the biology of *Orchestia* species and the abiotic factors limiting their distribution and density. No previous research could be found on the size and species composition of *Orchestia* on the east coast of Scotland and the factors determining density and distribution. Therefore, this thesis will begin by concentrating specifically upon the two *Orchestia*.

First, the population dynamics of *O. gammarellus* and *O. mediterranea* including a size comparison between species and sexes, and their population composition need to be determined, and how this varies between years. Second, evaluation of *Orchestia* distribution on the saltmarsh against biotic and abiotic influences will establish what drivers affect their presence and abundance in certain areas and habitats, and again how this varies between years. Finally, the capability of *Orchestia* to move and change location within the saltmarsh needs to be explored, and how they respond to the presence of redshanks, in terms of reducing overall abundance and distribution within micro-habitats as they move (or not) in response to predation risk.

2.1.1 Size and species composition

The size distribution of *Orchestia* may impact upon the distribution of feeding redshanks. This is because optimal foraging is employed by predators where they prey upon items that maximise their energy intake, in patches where prey density is greater or prey are larger, whilst spending the least amount of time searching and handling that prey (Werner and Hall, 1974). An example is the bluegill sunfish (*Lepomis macrochirus*) where when faced with a range of prey size (*Daphnia magna*), it selects larger individuals that satisfy its energy intake, so using less effort (Werner and Hall, 1974). Irons *et al*. (1986) found similar results for glaucous-winged gulls that preferentially selected larger barnacles and mussels, and Goss-Custard (1977a) found that redshanks selected larger *Nereis* worms, and *Corophium* (Goss-Custard, 1977b; 1977c) Therefore, when redshanks feed on *Orchestia*, they may purposefully feed in areas that contain the larger species and/or areas that hold more adults and/or, if the species is dimorphic, patches where the larger sex is more prevalent.

Previous research has shown variation in size (body length) between *O. gammarellus* and *O. mediterranea* and between the sexes. The maximum size of *O. gammarellus* in the Medway Estuary, southern England was given as 22mm (Wildish, 1988) and 17mm in the Baltic (Enckell, 1980). In the Medway, males were larger than females for both species, where the maximum size of *O. gammarellus* was 22mm for males and 18mm for females,

whereas for *O. mediterranea* it was 21mm for males compared to 19.5mm for females (Wildish, 1969). In the Ria Formosa saltmarsh in southern Portugal, the maximum size of *O. gammarellus* males was 17mm compared to 14mm for females (Dias and Sprung, 2004). However, these results contrast with research by Hurley (1956) who found that in five out of six terrestrial species of *Orchestia* in New Zealand, females were larger than males.

The composition of *Orchestia* populations is not standard throughout the year, or in different regions. Population composition for *O. gammarellus* was given as: juveniles 45%, females 32% and males 23% by Dias and Sprung (2004) on the Ria Formosa saltmarsh, who used pitfall traps and sieved cores of 113cm^2 to collect samples; whilst research in northwest France by Mantzouki *et al.* (2012) indicated a 50:50 split between males and females for samples collected in quadrats, but a bias towards females when caught in pitfall traps. Elkaïm, *et al.* (1985) described a 50:50 split in *O. mediterranea* in the Bou Regreg region of Morocco (quadrat collection), as did Wildish (1979) (randomly handpicked) for *O. gammarellus* in the Medway estuary. Research at Millport, on the west coast of Scotland, indicated that outside the breeding season when randomly handpicked, *O. gammarellus* sex ratio was 1.04:1 (male:female) whilst in the breeding season it was 0.62:1 (Moore and Francis, 1986b).

2.1.2 Distribution of *Orchestia*

Wildish (1969) suggested that *Orchestia* species composition on the shore is related to tidal coverage, where the species occupy different zones: *O. gammarellus* was to be found in areas above the recent high tide level, whereas *O. mediterranea* occurred in a distinct zone below that, although this was not due to differences in their chlorinity tolerance because experiments showed this to be similar for both species. Jones (1948) found *O. gammarellus* at high water springs level (HWS) and *O. mediterranea* at high water neaps (HWN) in Port Erin Bay, Isle of Man and similar findings were confirmed by: Den Hartog (1963), Rhine-Meuse-Scheldt delta region, Germany; Wildish (1972), Medway estuary; Bradley (1974), Duddon estuary, Cumbria; and Sprung and Machado (2000), Rio Formosa saltmarsh, Portugal. Nevertheless, there may be some overlap between the species because both have been found to occupy the high water springs position on the shore (Goodhart, 1941; Reid, 1947). Their behaviour when immersed in seawater may give an indication as to why they prefer separate habitats on the shore. Whilst *O. mediterranea* is content when covered by tides and swims strongly (Spicer *et al*., 1987), *O. gammarellus* avoids seawater at all costs; it is a poor swimmer and if submerged will swim vigorously for a while before sinking to the bottom and crawling out onto dry land (Henzler and Ingolfsson, 2007; Laffaille *et al*., 2005). Furthermore, salinity tolerance might explain why *Orchestia* inhabit different zones, nevertheless both appear similar in this respect. *O. gammarellus* can tolerate a wide range of sodium chloride concentrations to deal with freshwater runoff from the land and seawater inundation from high tides (Moore and Francis, 1986a; Charmantier and Charmantier-Daures, 2001). *O. mediterranea's* tolerance is like that of *O. gammarellus* and for both species Weeks and Rainbow (1992) found that there was very low mortality after 72 hrs when they were fed on food with a salinity range of 4 to 5 parts per thousand, and when immersed in seawater with the same salinity range.

Vegetation type may be important in *Orchestia* distribution. Saltmarsh vegetation consists of a series of halophytic vascular plants that occur in zones parallel to the shore (although this may be made more complicated by the incursion of creeks), where environmental tolerances dictate which species and communities are present (Adam, 1993). The study area is dominated by *Festuca rubra*, *Armeria maritima* and *Plantago maritima*

(henceforth *Pl. maritima*) in the outer marsh (the zone closest to terrestrial habitat that receives the fewest high tides), *Puccinellia maritima*, *Aster tripolium* and *Suaeda maritima* in the mid marsh (the zone that receives more high tides) and *Salicornia europaea* in the pioneer zone in the inner marsh (the zone that receives the most high tides) (Morris, 2005). Therefore, it might be expected that *Orchestia* distribution would be limited to species of vegetation that have a similar physiological tolerance of salinity and soil moisture. *O. gammarellus* occurrence has been associated with *P. maritima* by Den Hartog (1963) and Morritt and Ingolfsson (2000) and in *P. maritima* and *S. maritima* mixed habitat by Creach *et al.* (1997) and Moore and Francis (1985). There is no published evidence of *O. mediterranea* being linked specifically to any species of saltmarsh vegetation.

Vegetation structure may also be important in *Orchestia* distribution. For example, greater density of the sward may enable *Orchestia* to reduce the threat of desiccation and hide from predators. Colombini *et al.* (2013) in research carried out on the Maremma coast of Tuscany, Italy, suggested that *O. gammarellus* hides in the base of dense tussocks of *Juncus acutus* and *Schoenus nigricans*, specifically to escape drier weather in summer, whilst Pomeroy (1959) indicated that increased vegetation cover reduced evaporation by maintaining soil humidity so providing a suitable environment for species like *Orchestia* for whom drying out is a constant threat. Kraeuter and Wolf (1974) regard saltmarsh plant cover as paramount in protecting macro-invertebrates like *Orchestia* from predation from fish and birds. There might also be another reason that *Orchestia* inhabit thicker vegetation, because Colombini *et al.* (2013) discovered that *O. gammarellus* fed mainly on decaying plant material, specifically micro-algae and bacteria, and having a low circadian definition (little differentiation in activity and feeding levels throughout a 24-hour period), they stayed in situ and fed during daylight hours whilst remaining hidden from predators. In addition to overall sward density, sward height may characterise the habitat and give some indication as to *Orchestia* distribution, where it could provide protection from predating birds, whose feeding might be inhibited by the inability to focus on prey items in tall vegetation.

Seasonal effects may result in a general depression in numbers of amphipods on saltmarshes during the winter period (Sprung and Machado, 2000), and Ingolfsson *et al.* (2007) found that at Icelandic sites not heated by thermal springs, frozen ground resulted in very few individuals of *O. gammarellu*s being caught in pitfall traps. *O. cavimana*, a freshwater/brackish species, hibernates in winter (Dorsmann, 1935) and it is known that *Talitrus saltator* increases its burrow depth (Karlbrink, 1969) and possibly hibernates (Jones, 1948). However, Den Hartog (1963) found that *O. gammarellus* is active throughout the winter except in freezing weather, and Puttick (1984) mentions that on the Langebaan saltmarsh, South Africa, biomass and prey size of invertebrates increased in the winter, which enhanced curlew sandpiper *C. ferruginea* foraging success. In the study area, it is therefore expected that *Orchestia* are less obvious from November until the end of March, because they are deeper in the soil, quiescent and harder to detect.

On a longer timescale, inter-annual changes in *Orchestia* abundance and distribution may be influenced by the success of the breeding period. At Millport on the Isle of Cumbrae, west coast of Scotland, Moore and Francis (1986b) found that ovigerous females of *O. gammarellus* began to be seen at the end of April when temperatures reached around 7°C and breeding continued until September. They went on to suggest that initiation of breeding occurred in tandem with extension of the photoperiod of light:dark – 14:10hrs. Wildish (1969, 1979) indicated

previously that *O. mediterranea* had a similar breeding period to that of *O. gammarellus* but did not say what initiated this. However, the importance of the photoperiod has been rejected both by Morritt and Stevenson (1993) in research on again at Millport, Isle of Cumbrae, and Persson (1999) in the Kalmar Sound, southern Baltic. Therefore, if temperature is the sole cause of breeding initiation, a colder spring could delay and reduce recruitment to the population for that year.

In addition, if *Orchestia* species are associated with a specific type of vegetation or community, changes in the composition and occurrence of this could affect *Orchestia* distribution on an inter-annual basis. Vegetation succession on saltmarshes takes place over many years (Schrama *et al*., 2012) and it may take decades for a vegetation community to change, although stochastic weather events can cause extensive damage and very cold winters may lead to local extinction of some species (Adam, 1993). Packham and Liddle (1970) discovered that on the Cefni saltmarsh, Anglesey, abundance changed markedly across a period of 13 years for common species such as *A. maritima*, *F. rubra* and *P. maritima*. Therefore, although saltmarsh cover and topography may seem to alter very little over a generation, this might not be the case (Packham and Willis, 1997). A change in the species present and number of *Orchestia* inhabiting an area from year to year, may then also impact upon the feeding distribution of redshanks.

Finally, variation in micro-topography may also affect Orchestia distribution. For example, on the Duddon estuary saltmarsh, Cumbria, Bradley (1974) found that *Orchestia* were particularly numerous on the cliffs of creeks and under the loose turves at their edges, which was also noted by Den Hartog (1963) in the Deltaic region of the Netherlands. Initial investigation in the study area suggested that *Orchestia* prefer areas of the saltmarsh that are adjacent to creek edges. Because the soil is prone to erosion from tides and produces fissures, *Orchestia* congregate here where they may be sheltered from extremes of temperature and the drying effect of the wind, which can alleviate desiccation stress. Fissures may also provide security from predation by birds and fish.

2.1.3 *Orchestia* behaviour: dispersal, displacement and movement

Orchestia need a means of movement to find breeding partners, colonise new areas, and to avoid predators and this is achieved by both passive and active dispersal (Dahl, 1946). Passive dispersal is where *Orchestia* are displaced by the tide over a wider area, whereas with active dispersal they use their own locomotion to explore the local habitat (Wildish, 1988). *O. gammarellus* has limited control over its movement in the tide, and its surface mobility is poor compared to other species (Colombini *et al*., 2013). Because it has poor swimming capabilities and avoids seawater if possible (Karlbrink, 1969), at high Spring tides mass migrations of *O. gammarellus* can be seen moving out of macro-algal detritus on the strandline to the safety of the supralittoral zone (pers. obs.). *O. mediterranea* on the other hand is one of the few Talitridae that has some control over its own movement in seawater, where it propels itself forward by beating its pleopods. Moreover, passive dispersal enables *Orchestia* species to cling onto pieces of floating debris until they are deposited to colonise new areas of coast (Spicer, *et al.*, 1987). There has been limited research into how much displacement of *Orchestia* occurs across a saltmarsh, during both tidal inundation and intertidal periods.

Movement characteristics are important with respect to the response of *Orchestia* when being targeted as prey,

particularly by redshanks in the study system. When disturbed, *Orchestia* jump randomly (Sars, 1890; Williamson, 1951) up to four times before they either become quiescent if they land in suitably moist conditions, or crawl to find such conditions under vegetation, wrack or in soil (Wildish, 1969). *Orchestia* availability for feeding redshanks may then be reduced even in profitable areas due to what Charnov *et al*. (1976) term *microhabitat depression*, where prey change position and become harder to locate. This has been observed in clams (*Mya arenaria*) which bury deeper when facing predation from red rock crabs (*C. productus*) (Zaklan and Ydenberg, 1997); redshanks, where interference amongst conspecifics forces *Corophium* to burrow deeper (Goss-Custard, 1980; Stillman *et al.*, 2000); and specifically at the study site where *Orchestia* are forced to retreat deeper into the soil by redshanks moving through an area (Minderman *et al.*, 2006). Therefore, redshank disturbance can impact *Orchestia* distribution in a second dimension; on the vertical plane, and so diminish their availability. Such anti-predation behaviour may however also be species specific. The jump of *O. cavimana*, a morphologically similar species to *O. gammarellus* and *O. mediterranea*, has been timed at 350-400 m/s, over 18cm, where the initial acceleration was 300 m/s^{-2} (Bracht ,1980), but Karlbrink (1969) states that *O. gammarellus* is a poor jumper compared to other *Orchestia*. Redshanks may also affect *Orchestia* density and distribution by depleting numbers throughout the winter through density mediated effects: compared to a trait-mediated effects, where intimidation affects resource density and distribution following anti-predation strategies by prey which alter their behaviour. The two were compared in general terms by Bolnick and Preisser (2005) and Preisser *et al*. (2005), and both effects were discovered to be equally strong in the same system. This was also found by Schmitz and Suttle (2001) where a grasshopper species reacted through a DMI or TMI effect, but was dependent upon which of three species of spider was depredating it.

Any active movement may be affected by temperature because *Orchestia* are likely to be more active at higher temperatures. However, Dias and Sprung (2004) found that for *O. gammarellus,* between air temperatures of 7°C and 20°C, this was not the case. In contrast, *T. saltator*, a species similar in morphologically to *Orchestia*, the increase in surface activity was correlated to an increase in air temperature (Williams, 1980; Scapini *et al*., 1996), sand temperature and wind speed (Scapini *et al*., 1996).

2.1.4 Objectives

Because there is little previous research regarding the size, composition, extent, distribution and behaviour of *Orchestia* on saltmarshes in the British Isles, this chapter will investigate this to enable a better understanding of their importance in this ecosystem.

Size and composition of Orchestia

1. Prior research on size between species is conflicting, so samples will be taken of both *O. gammarellus* and *O. mediterranea* to determine this. Initial investigation suggests that generally, *O. gammarellus* will be larger than *O. mediterranea* and the species will be sexually dimorphic with males being larger than females.

2. The composition of *Orchestia* appears to change throughout the year, so samples should determine what the ratio of males:females and adults:juveniles is in winter for each species. The results of this cannot be predicted because previous research is contradictory.

3. Size will also be investigated in redshank feeding and non-feeding areas. It is expected that redshanks purposefully forage in areas which hold larger *Orchestia* species and/or areas which hold the largest individuals.

4. Redshank feeding plots will be visited after birds have moved away and *Orchestia* taken for species identification, sizing and sexing. It is hypothesised that foraging redshanks will have taken larger *Orchestia* so the plot will be revisited to determine if there is a difference in size, unless feeding areas have been replenished by larger *Orchestia* between the first and second visits.

Distribution of Orchestia

5. The number of tides and extent of tidal coverage will be measured in conjunction with the presence and abundance of *Orchestia* to determine how tides determine their distribution. It is predicted that *O. gammarellus* will occur in the outer saltmarsh at higher elevations, whereas *O. mediterranea* will prefer the mid and inner saltmarsh at lower elevations, although there may be an interface zone where both occur.

6. Distance from the nearest creek edge will be measured to confirm that *Orchestia* prefer this habitat and it is hypothesised that *Orchestia* will be more likely to be present and abundant the nearer they are to creek edges.

7. *Orchestia* may become less active in winter, hiding in the subsoil during colder periods, so changes in occurrence and abundance will be tested over this period. It is predicted that *Orchestia* will be found in the subsoil in colder weather and higher wind speeds especially in the midwinter, but are more likely to be on the soil surface and more available to redshanks in late autumn and early spring.

8. The preference of *Orchestia* for specific species of halophytic vegetation will be recorded. The type of vegetation they occur in should resemble their own tolerances to salt and seawater coverage. Therefore, it is hypothesised that presence and abundance should increase along with an increased density in their preferred vegetation.

9. *Orchestia* abundance against the density and height of the sward overall will be tested. It is hypothesised that they will prefer denser vegetation to hide from predators, to reduce the effects of desiccation, and may also prefer higher vegetation where predators have greater difficulty in locating them.

10. *Orchestia* distribution and density may change between winters. An association of *Orchestia* distribution between two winters will be tested where a comparison of 100 randomly chosen sample plots from winter 1 will be revisited in winter 2 to confirm that *Orchestia* are still present and that the same species occur. It is predicted that two consecutive winters should show little change unless there has been a major storm which might cause major change to the topography of the saltmarsh.

Orchestia behaviour

11. The dispersal of *Orchestia* using covered and uncovered plots, where a mark-recapture experiment will determine whether *Orchestia* are moved passively by the tide and/or if they disperse by their own means. It is predicted that tidal coverage will have the greater effect, where they are transported out of the immediate area.

12. Prey resource depression will be examined, where *Orchestia* will be counted in surface plots immediately after redshanks have left a feeding area and again later, to confirm whether feeding birds have depressed *Orchestia* numbers. It is predicted that this will be the case, making them temporarily unavailable to redshanks.

13. The effect of weather on the type of *Orchestia* movement, and speed of movement will be tested. This will specifically look at the effects of temperature and wind speed. It is predicted that *Orchestia* will crawl and jump more in warmer temperatures and when the wind speed is reduced, and in warmer temperatures movements should be quicker.

2.2 Methods

2.2.1 Study site

The study site is at Tyninghame, 4.63 km west north west of Dunbar in East Lothian, Scotland. It covers 31 hectares and is made up of saltmarsh, estuarine mud and sand. It is roughly triangular with the apex pointing north and is demarcated to the west by Little Binning Wood, to the east by a spit which extends south east – Sandy Hirst, and to the south by an estuary leading out from the River Tyne at Mosshouse Point. The shoreline east of Sandy Hirst is Tyne Sands where the lower shore is of sand and mud and the upper of bedrock and boulders. The northern apex is at 56°00'57.66"N, 2°35'30.66"W, the southeast point at 56°00'28.96"N, 2°35'07.01"W, and the southwest at 56°00'25.23"N, 2°35'42.43"W. The saltmarsh contains many creeks and the main channel begins close to the apex and runs south until it enters the estuary 150m to the west of Sandy Hirst (Figure 2.1).

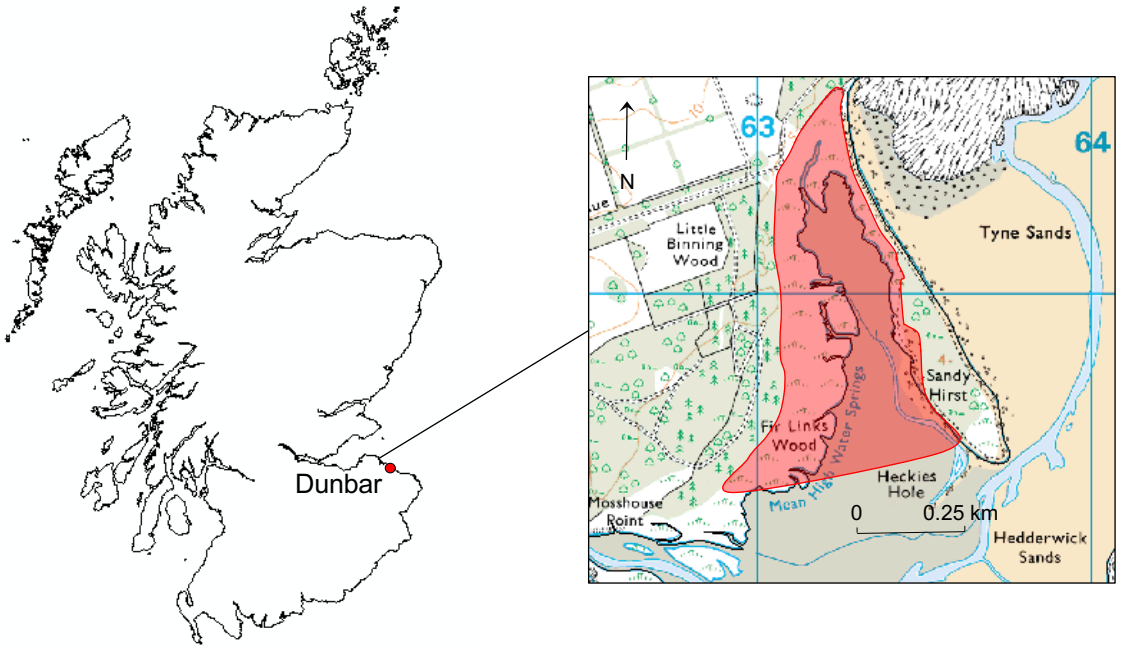


Figure 2.1 *The study site at Tyninghame (OS MasterMap Topography Layer, 2011; OS 1:25; 000 Scale Raster, 2016)*

2.2.2 *Orchestia* sampling protocols

The research study took place between November and March over three winters, 2013/14 (winter 1), 2014/15 (winter 2) and 2015/16 (winter 3). Day number was used instead of calendar date to record the day of the fieldwork visit (*e.g.* winter 1: day 1 = 11 Nov 2013 – day 134 = 24 Mar 2014). Most of the fieldwork regarding *Orchestia* distribution was conducted in winter 1. First, 300 random points (sample plots) were created using ArcGIS Create Random Points Tool, utilising a digitised polygon of the study area as the constraining feature for the random points (ESRI, 2013). The 300 points were again randomised using a true randomisation programme at Random.org (Haahr, 2013) to produce a plot order. A maximum of 20 plots could be visited in a daily fieldwork session, which produced 15 fieldwork visits between 11 Nov and 22 Dec 2013. Plots were uploaded into and Active 10 Satmap handheld GPS that gave an accuracy of ± 2m, but in tests accuracy was occasionally reduced

to ± 3-4m due to low satellite coverage. It was necessary to sample a wider area on the estuarine and creek mud initially to determine if *Orchestia* occurred in *Pelvetia canaliculata* as suggested by Minderman *et al*. (2006), or on other macroalgal deposits. Once fieldwork of the first 300 points had been completed, it was discovered that 63% of the plots either occurred on mud in the estuary, between the southern projections of the saltmarsh, or in muddy creeks and no *Orchestia* were found (Figure 2.2 - left).

Figure 2.2 *Left – the first 300 random sampling points where all areas were sampled including estuary mud. Right – random sampling points 301-700 where stratified random sampling levels were used, omitting sampling effort on the estuarine mud due to no Orchestia being found here.*

To rectify this, another 400 points were configured (numbers 301 – 700) using the same procedure as above, except that a new constraining feature of the study area was digitised, omitting the estuary area that had returned no *Orchestia*. Second, random points were split into three distinct areas of outer, mid and inner saltmarsh that enabled stratified random sampling (Figure 2.2 - right). The 20 plots visited on each fieldwork session were randomised again and consisted of 7 outer, 8 mid and 5 inner plots, where the number of plots equated to the size of the stratified area. The 20 fieldwork visits for this second stage took place between 7 Jan and 24 Mar 2014.

2.2.3 Measuring size and composition of *Orchestia*

To complete objectives 1 to 4 of this chapter, identification and sizing of *Orchestia* species was necessary and carried out over all three winters, using the protocol in Figure 2.3 (see also accompanying images 2.3a and 2.3b).

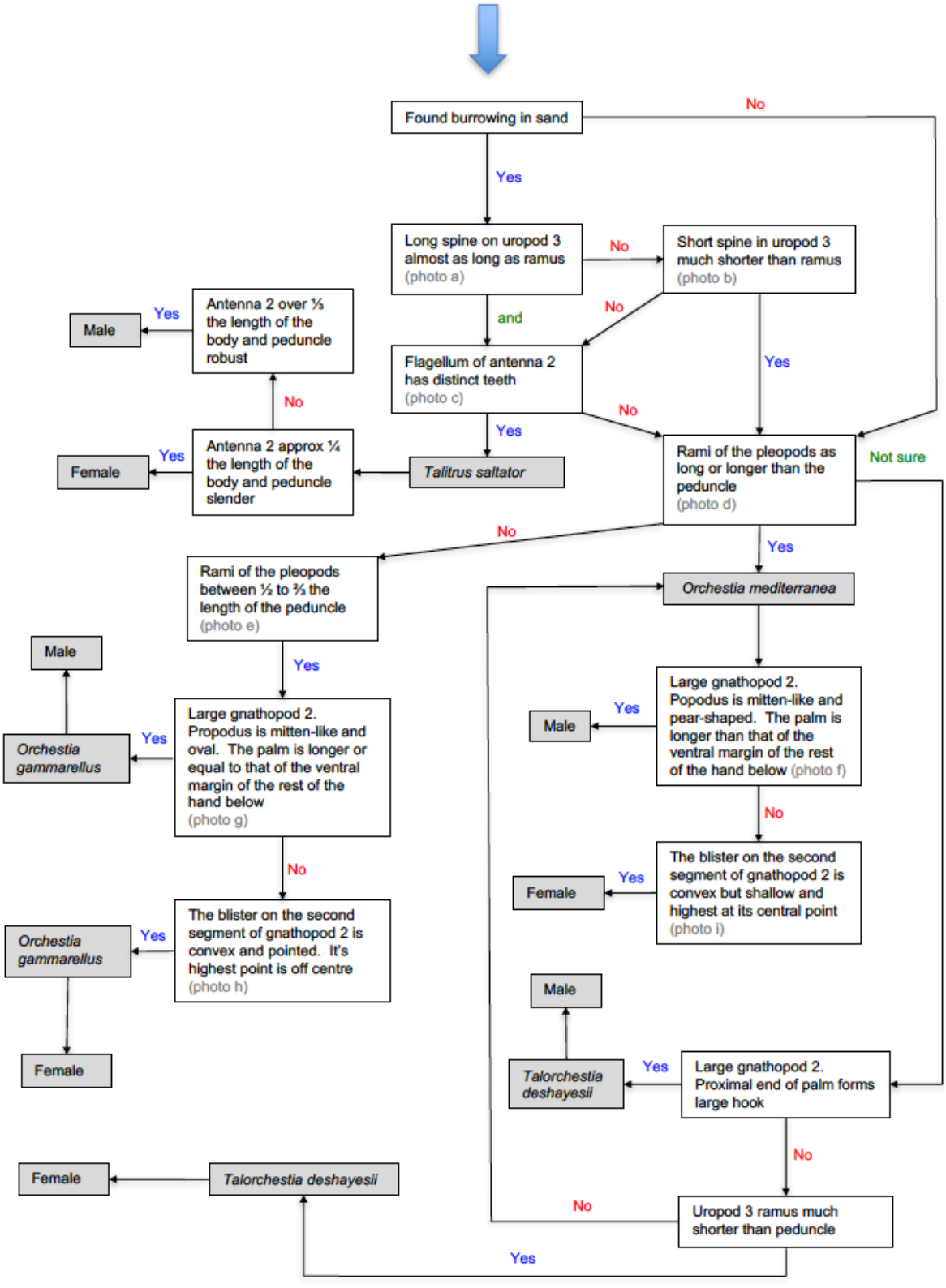


Figure 2.3 *Differentiating the four species of Scottish sandhopper found at the study site* (O'Reilly 2011). *Systematics of identification taken from Reid (1947), Lincoln (1979), Wildish (1988), Hayward and Ryland (1990), Spicer and Janas (2006). Diagnostic photographs are shown in Figures 2.3a (photos a-c) and 2.3b (photos d-i).*

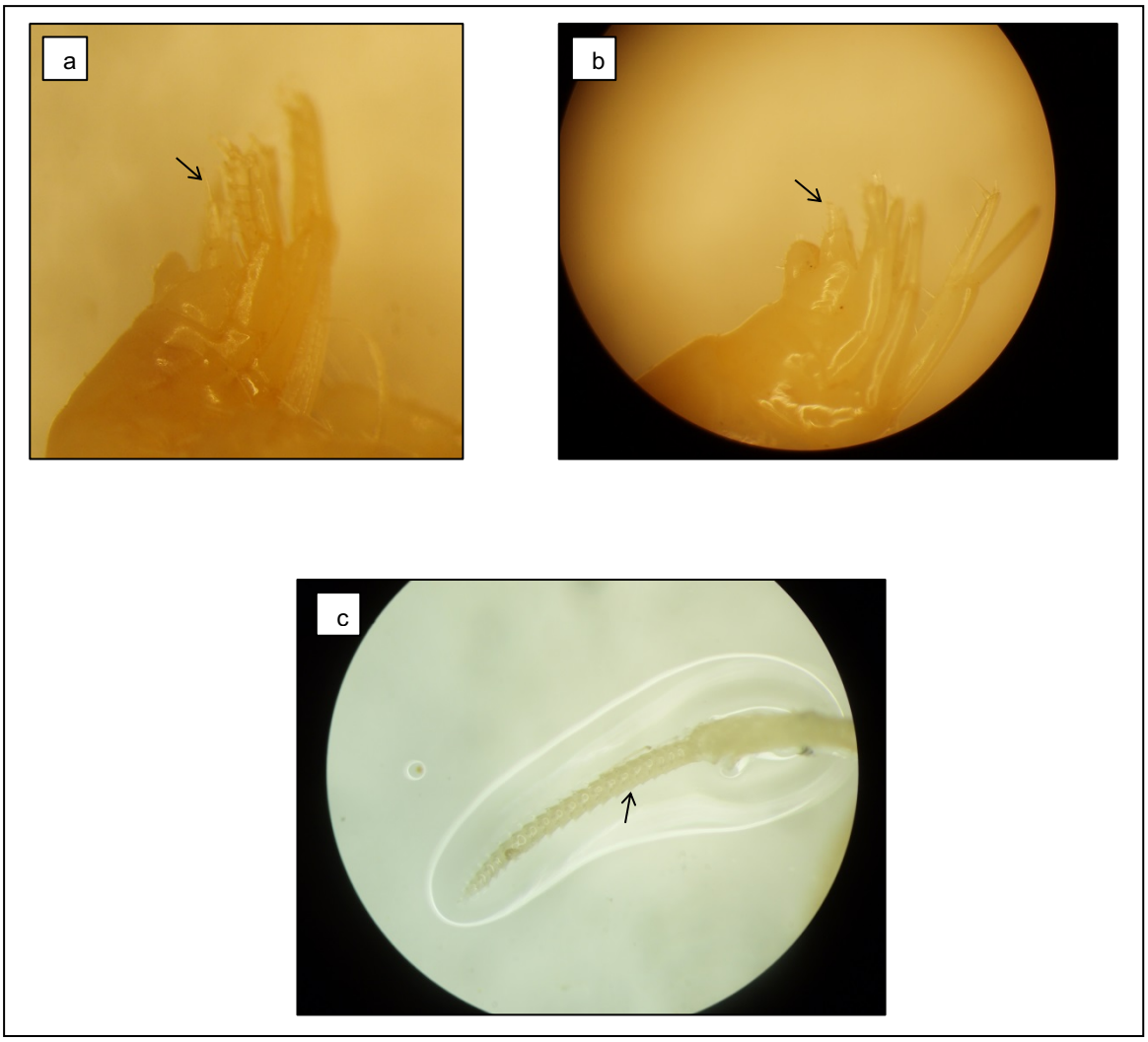


Figure 2.3a *Diagnostic features of sandhopper identification. a. Long spine of uropod 3 indicating Talatrus saltator. b. Small spine of uropod 3 indicating Orchestia/Talorchestia. c. Distinct teeth on flagellum indicating T. saltator.*

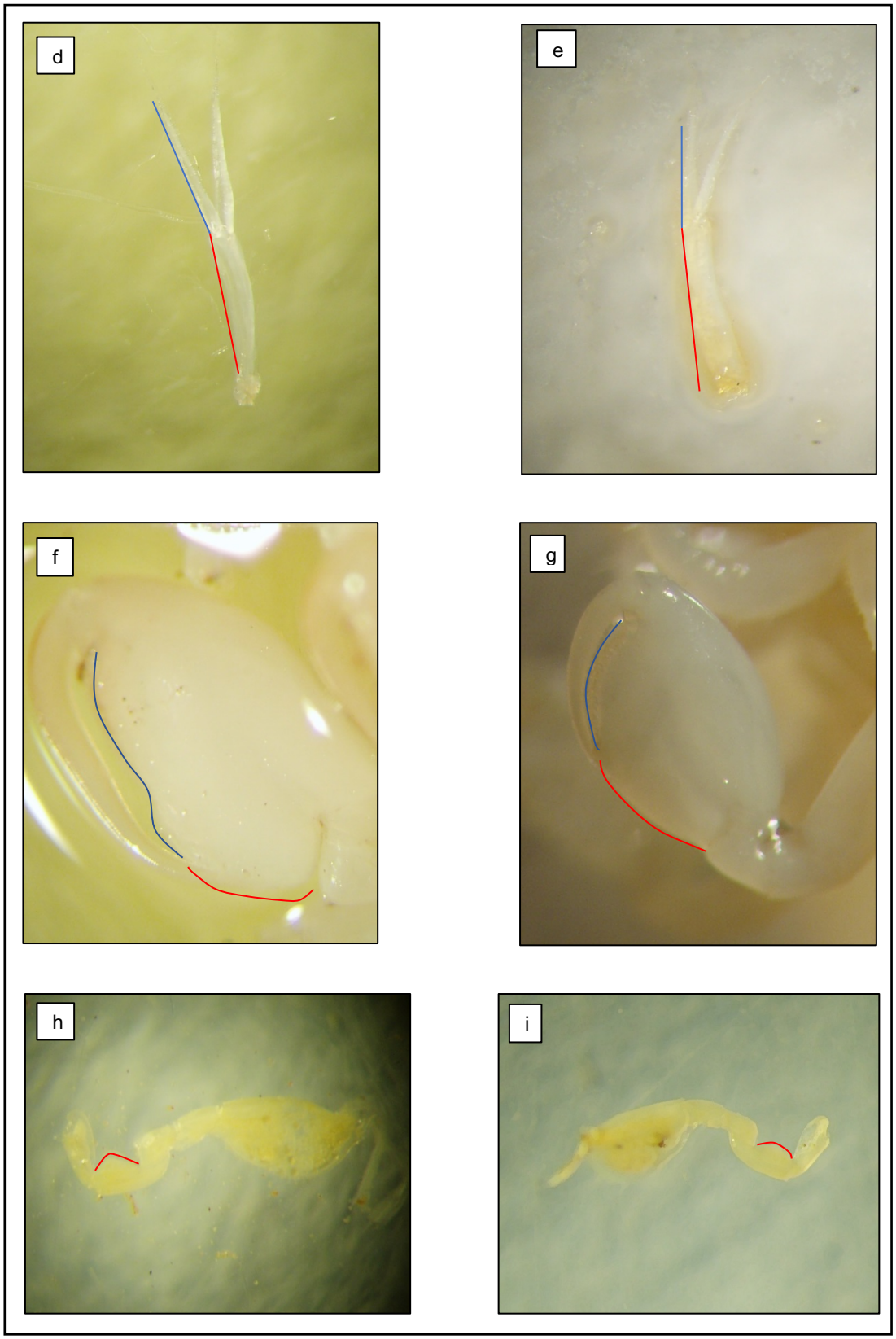


Figure 2.3b *Diagnostic features of sandhopper identification (cont). d. Rami as long as peduncle of pleopod – O. mediterranea. e. Rami longer than peduncle of pleopod – O. gammarellus. f. Second gnathopod pear-shaped, long palm – O. mediterranea male. g. Second gnathopod oval, short palm – O. gammarellus male. h. Blister on second gnathopod convex, but apex off centre – O. gammarellus female. i. Blister on second gnathopod convex but flat, apex central – O. mediterranea.*

Size was taken from the cephalon to the tip of the telson, to the nearest 0.5mm. Wildish (1969) made a distinction between juvenile and immature *Orchestia* (immatures possess proto reproductive organs), but Rossano and Scapini (2009) and Ingolfsson *et al*. (2007) termed all those without adult morphological features as juveniles. In this research, quite often individuals between 8mm and 9mm had proto morphological features that enabled sexing. These features included swelling of the mitten on the second gnathopod (male), or the shape of the second segment of the second gnathopod (female). Occasionally individuals under 8mm also had these features so could be sexed and classed as juveniles. Ingolfsson *et al*. (2007) decided that the criteria for a juvenile was any individual under 9mm in length. This research will categorise juvenile *Orchestia* as individuals less than 8mm in length. Juveniles of *O. gammarellus* and *O. mediterranea* were distinguished by differences in the rami and peduncle lengths of the pleopods, a feature described by Wildish (1972, 1987) (Figures 2.3, 2.3a and 2.3b).

Statistical analyses for size (objective 1) were modelled using a Gaussian GLM where size in mm was the response variable and species of *Orchestia*, sex and winter were entered as the predictor variables along with their interactions. As the predictor variables were entered as factors a Tukey post-hoc test was used to indicate which were significantly different from one another. For objective 2, Chi-squared tests (Pearson) were used to compare the composition between (1) males and females and (2) adults and juveniles of each species, to test the null hypothesis that there was no significant association between the categorical variables.

Size of Orchestia in redshank feeding and non-feeding areas

Objective 3. In winters 2 and 3 *Orchestia* were collected from plots (N = 108) visited immediately after redshanks had been disturbed and flown off, to determine whether *Orchestia* were larger in foraging areas. Redshanks had been foraging in these areas from between 5 and 40 minutes. A 1m x 1m quadrat was used and *Orchestia* found on the surface were taken for species identification, sizing and sexing. Vegetation type, overall vegetation density and vegetation height were recorded. These were then compared with 1m x 1m quadrats from non-feeding areas over winters 2 and 3 (N = 220). Generalised Linear Mixed Models (GLMM) were used from the nlme package (Pinheiro et al., 2015) to model all *Orchestia* and then each species separately, where plot number was used as a random factor. The models were fitted to maximum likelihood (ML) initially to enable accurate comparison of fixed effects between models. Restricted maximum likelihood (REML) was then run in the best model which gave more accurate estimates (Rendhal, 2013).

Size of Orchestia size in revisited feeding plots

To undertake objective 4, surface samples of *Orchestia* were taken from 26 plots using the 1m x 1m quadrat in winter 2, immediately after redshanks had been disturbed and flown off. Redshanks had been foraging in these areas from between 5 and 40 minutes. This was to test whether redshanks preferentially chose larger *Orchestia* when moving through a patch. Revisits were conducted on the same plots between one and six days later; in that time, some had had tidal coverage, and some had not. It was therefore expected that *Orchestia* would re-inhabit a foraged patch, either returning by their own means, or passively transported by the tide. Statistical analyses were conducted using GLMMs as per the size of *Orchestia* in redshank feeding and non-feeding areas experiment.

2.2.4 Sampling of Orchestia *distribution*

Two quadrats were used at the sample plot position. During winter 1, variables that might influence *Orchestia* distribution were measured using a 1m x 1m quadrat. These included: vegetation cover and height, distance from the nearest creek edge, the influence of weather on distribution, and tides and elevation (objectives 5-10). A second 10cm x 10cm quadrat was placed in the centre of the larger one. A turf was cut out the same size as this quadrat down to a depth of 6 cm and *Orchestia* were taken for later identification, sizing and sexing. On rare occasions, *Orchestia* might occur deeper than 6 cm, especially in sandy soil inhabited by *F. rubra*, so exploration continued to a depth where no more *Orchestia* could be found. Distance from the nearest creek edge was measured to the centre of the smaller quadrat. The fieldwork measuring changes in density and distribution of *Orchestia* between winters 1 and 2 (objective 10) used the same methodology. For further details see page 38.

Tides and elevation

To address objective 5, in winter 1, *Orchestia* presence and distribution was measured with regard to the amount of tidal coverage. Times and heights of high tides for fieldwork were taken from Dunbar 3 miles to the south east. High tide levels on the saltmarsh were measured for later statistical analysis and this was done by walking a route around the extent of the high tide with the handheld GPS. The information was then uploaded into ArcGIS and high tide levels were digitised and collated into 13 polygons. Therefore, polygon 1 was the area covered by a high tide <4.5m, polygon 2 was a high tide 4.5m - 4.59m, polygon 3 was a high tide of 4.6m - 4.69m, and so on up to polygon 13 which was high tides >5.6m. The number of high tides per annum could then be evaluated for each polygon (Table 2.1).

Table 2.1 *Number of high tides per annum in 13 designed area polygons*

High tide area	High tide height (m)	Number of high tides per annum in each polygon	Total number of high tides per annum
1	< 4.5	154	708
2	4.5 – 4.59	48	554
3	4.6 – 4.69	48	506
4	4.7 – 4.79	53	458
5	4.8 – 4.89	50	405
6	4.9 – 4.99	51	355
7	5.0 – 5.09	58	304
8	5.1 – 5.19	53	246
9	5.2 – 5.29	59	193
10	5.3 – 5.39	38	134
11	5.4 – 5.49	28	96
12	5.5 – 5.59	24	84
13	> 5.6	44	44

Objective 5 also predicted that *O. gammarellus* would prefer higher areas and *O. mediterranea* lower areas of the saltmarsh. Therefore, in winter 1 elevation was measured over three days in winter 2 using a Promark™ 120 Global Navigation Satellite System (GNSS) with a vertical accuracy of ± 2cm. This equipment consists of a base station placed in the centre of the saltmarsh and handheld rover module that could be positioned to give one reading/minute. Measurements were taken across the study site in transects from the outer to inner marsh. Points and transects were roughly 15m apart. Points were then downloaded as a Microsoft Excel version 15.30 (2013) table into ArcGIS (ESRI 2013) and a digital elevation model (DEM) constructed. This was achieved by making shapefiles of the points and of the saltmarsh boundary. The DEM was then built from the two shapefiles using 3D Analyst Tools > Raster Interpolation > Topo to Raster > Feature Layer of point shapefile = Type: Point Elevation > Feature Layer of saltmarsh boundary shapefile = Type: Boundary > field = Alt for both shapefiles > Output Surface Raster = filename > Output Cell Size = 3.12 (Childs, 2004; ESRI, 2013). From this DEM an elevation reading could then be extracted for any point, such as an *Orchestia* sample point on the DEM layer by the following procedure: ArcToolbox > Spatial Analyst Tools > Extraction > Extract Multiple Values to Points (ESRI 2013) (Figure 2.4). These values could then be exported into the Microsoft Excel data file used to run models in R Studio statistical software (R Studio Team, 2015).

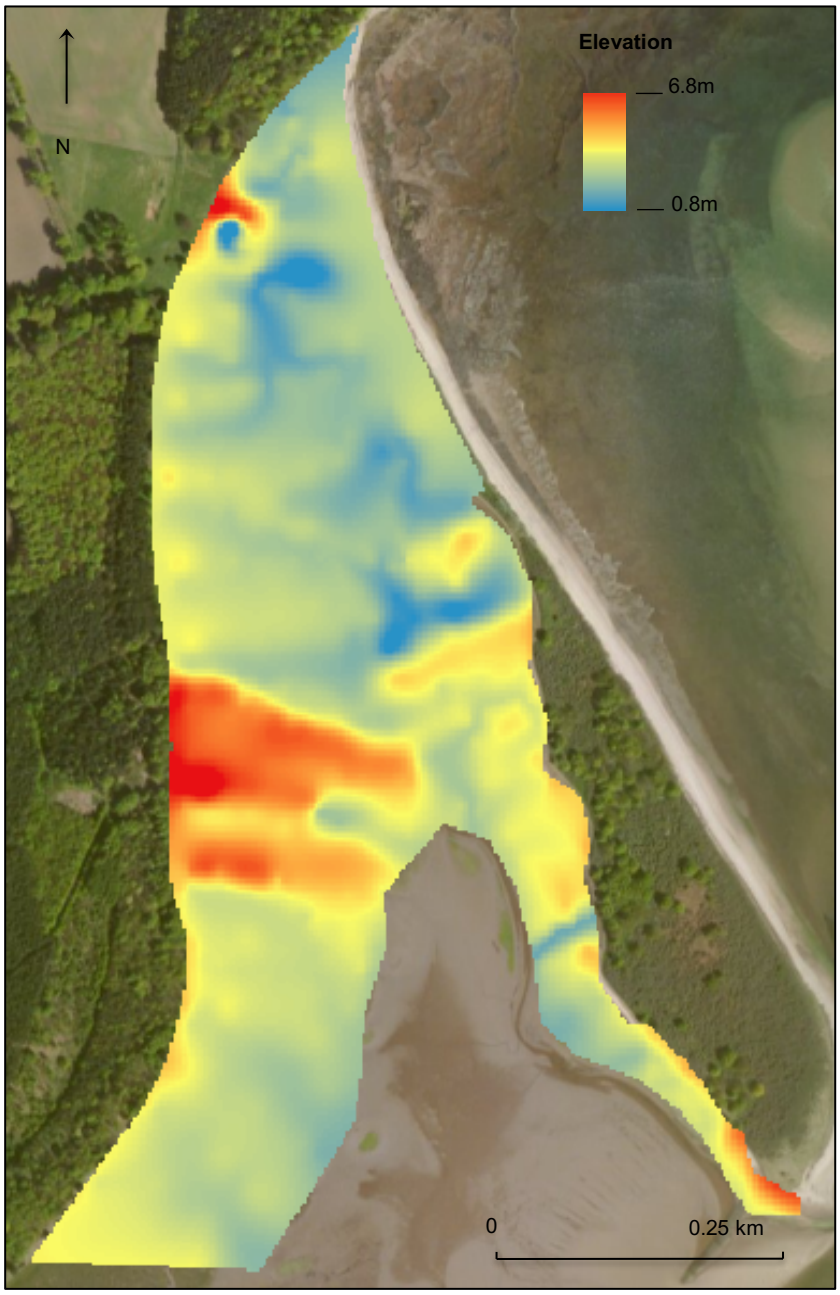


Figure 2.4 *Digital Elevation Model of the study area. Elevation points measured using GNSS and entered into ArcGIS software* (ESRI, 2013) *to produce a raster-based elevation layer.*

Distance from the nearest creek edge

Objective 6 predicted that *Orchestia* are more likely to occur and be more abundant close to creek edges, so part of the fieldwork in winter 1, was to measure the distance from the centre of the quadrats to the nearest creek edge using a 50m tape measure. If the distance was over 50m the distance was measured using the handheld GPS.

The influence of weather

To determine if weather influenced *Orchestia* distribution, air temperature and wind speed were recorded using a hand held mini weather station positioned 1m above the ground surface in the centre of the quadrats (objective

7). An ATP DT-610B laboratory thermometer was used to take the soil temperature to a depth of 1cm in the centre.

Vegetation composition, overall vegetation density and height

To measure vegetation coverage and height, the 1m x 1m and was used to estimate percentage coverage of each species of vegetation in the quadrat (objective 8). The overall vegetation density was estimated along with the height of vegetation. This was taken by averaging of the height measurements from each of the four corners and the centre of the quadrat (objective 9).

Statistical analysis of Orchestia distribution

Determining distribution is fundamental to understanding ecosystems and their management and this is often done by measuring presence and absence rather than abundance which is more difficult (Estrada and Arroyo, 2012). It is suggested that although presence/absence modelling readily identifies areas of the highest densities of a species, randomness or evenness in spacing of that species can only be determined by conducting abundance counts (Estrada and Arroyo, 2012). Therefore, in this research both methods were employed to predict distribution of *Orchestia*. Data were entered into Microsoft Excel version 15.30 (2013). Analyses were then carried out using the statistical software RStudio (2015). Rejection of the null hypothesis was at the <0.05 level.

Modelling for presence/absence

First, analyses were done for *O. gammarellus* and *O. mediterranea* separately investigating their probability of occurrence. Predictor variables regarding vegetation, distance to the nearest creek edge, weather, tide, elevation were entered into models with the number of *Orchestia* as the response variable. Presence/absence models were fitted for the binary data where 1 = present and 0 = absent. In this, pi is the probability of success (*i.e.* equals 1 not 0), so the mean = p and variance = p*(1-pi) (Thomas *et al*., 2015). Therefore, generalised linear models (GLM) were used where the predictor variable was not continuous and errors were non-normal and binomial was used as the error family (Thomas *et al*., 2015). The *corvif* function calculated variance inflation factors (VIF) for all model structures to check for predictor variable collinearity (Zuur *et al*., 2009), where a VIF of over 3 was assumed to be collinear. If this was the case, then the variables that were collinear were modelled separately. (Thomas *et al.*, 2015). Although *P. maritima* and vegetation density were collinear with VIFs of 3.6 and 3.9 (*O. gammarellus*) and 3.04 and 3.8 (*O. mediterranea*) respectively, *P. maritima* was dropped from the modelling process at an early stage in both models as a non-significant term. In the *O. gammarellus* model, high tide areas were pooled which produced a better model, where 4.7m – 4.89m was entered as high tide area 1 and <4.7m and >4.89m became high tide area 2. Similarly, for *O. mediterranea* high tide areas were also pooled so that <4.7m and >4.99m became high tide area 3 and 4.7m – 4.99m, high tide area 4. Model evaluation and predicting accuracy of the model was estimated using the PresenceAbsence package (Freeman and Moisen, 2008) to check various parameters including: PCC – proportion of test observations correctly classified; kappa – standard deviation; sensitivity – proportion of observed positives correctly predicted; specificity - proportion of observed negatives correctly predicted; and AUC – Area under curve, an independent measure of model quality (Freeman and Moisen, 2008). Occasionally, the code to extract these produced an error, but a modified code from the same package

gave the PCC only. Models were also compared with AIC (Akaike Information Criterion), which is a measure of goodness of fit of similar models, but to achieve that fit the number of parameters are penalised. The smaller AIC value means a model with a better fit (Zuur *et al*., 2007; Thomas *et al*., 2015). Pseudo-R^2 values were checked along with residual plots to validate models.

Modelling for abundance

These models measured changes in numbers of *O. gammarellus and O. mediterranea*, separately. VIFs were calculated to test for collinearity of predictor variables as above, but none were collinear. The distribution of the predictor and response variables was investigated and in some cases a Shapiro-Wilk test was conducted to give an indication of normality, although where $n >$ approx. 30 the test is so powerful that it detects very small deviations (Thomas *et al*., 2015). Therefore, Shapiro-Wilk was used as a guide with more importance being given to visual plots of the data. If nil counts were included in the models this caused a zero inflation problem where the response variable contained an excessive number of unexpected zeros for a poisson distribution (Zuur *et al*., 2009). In this instance, because presence/absence models had already analysed the nil count influence of probability, zeros in the data were removed leaving just positive integer counts. These were then analysed using a GLM with a poisson distribution. To validate models fitted the data, R^2 and adjusted R^2 values were compared along with residual plots. In contrast to presence/absence models, for both *Orchestia* species the best models were ones where tide was entered as a continuous rather than a categorical variable - *total number of high tides per annum* (per high tide area polygon – 1-13).

Changes in distribution and density between winters

It was predicted that *Orchestia* distribution and density may change annually (objective 10), so the distribution of *Orchestia* was compared between winters. A selection of points was revisited to check that *Orchestia* were still present, and that the same species occurred. This took place between winters 1 and 2, so the 400 points from the second stage in winter 1 were randomised using the same true randomisation procedure as before - Random.org (Haahr, 2013). Then the first 35 outer, 40 mid and 25 inner points were taken off the randomised list, which again reflected the size of each area, and enabled stratified random sampling of the 100 points to be revisited. This fieldwork took place in winter 2, between 11 Nov 2014 and 24 Feb 2015. Because the data were non-normally distributed, a poisson GLM was used to model each *Orchestia* species independently using the same statistical procedures as detailed in *Modelling for abundance* on page 37.

2.2.5 Sampling and statistical analyses of *Orchestia* behaviour

Four experiments were carried out to determine the behaviour of *Orchestia* under the influences of tide (dispersal), redshank disturbance, and the impact of weather on movement and speed of movement.

Dispersal experiment

This experiment relates to objective 11 which predicted that tidal coverage will transport *Orchestia* out of their immediate habitat. Before the main mark-recapture experiment could take place, a pilot study was conducted to determine if: marking with varnish killed the *Orchestia*; varnish rubbed off; the plastic boxes remained in situ;

the time between marking and recapture affected numbers recaptured; and wet sieving of the removed turf found more marked *Orchestia*. From seventeen experimental plots, 8 received no tidal coverage and 9 did, the time between release and recapture varied between 4 and 120 hours, and 10 were sieved whilst 7 were wet sieved. The data for this experiment are shown in Table 2.2.

Table 2.2 *Data for pilot experiment showing the mean percentage of marked Orchestia recaptured for tidal coverage and non-tidal coverage, and sieving versus not sieving.*

Variable	N of plots	Mean % of marked *Orchestia* recaptured	SE
Plot covered by high tide	8	84.16	4.35
Plot not covered by high tide	9	82.79	1.92
Recaptured *Orchestia* wet sieved	10	84.66	3.59
Recaptured *Orchestia* not sieved	7	81.68	1.81

Results showed that *Orchestia* survived the marking, although it was possible that a small number of individuals managed to rub the varnish off. The number of marked *Orchestia* recovered showed a normal distribution and no collinearity, so analysis was conducted using a Gaussian GLM with an identity link function (Thomas *et al*., 2015). Varnish did not kill the *Orchestia* and although some of the varnish spot occasionally rubbed off, enough remained to identify the *Orchestia* as a marked individual upon recapture. The effect of time between release and recapture showed no significant effect. The effect of sieving versus non-sieving showed a significant effect, where sieving increased the numbers recaptured by 17% (Table 2.3 and Figure 2.5).

Table 2.3 *The best linear model for the pilot study which looked at the effect of time on the recapture of marked Orchestia and the merits of sieving versus non-sieving. The total originally marked was entered as a log offset.*

Variable	Estimate	SE	*t*	*P*
Intercept	17.52	2.27	7.7	**<0.001**
Time between release and recapture	0.09	0.07	1.2	0.253
Wet sieved	7.86	2.77	2.8	**0.013**
Time before recapture*wet sieved	-0.16	0.08	-2.0	0.064

Significant *P* values are marked in bold. The intercept also includes not sieved *Orchestia*. The Adjusted R^2 for this model is 0.32. Degrees of freedom 13. Best model AIC: 87.9, full model AIC: 92.6. Variable removed from full model - number of tides.

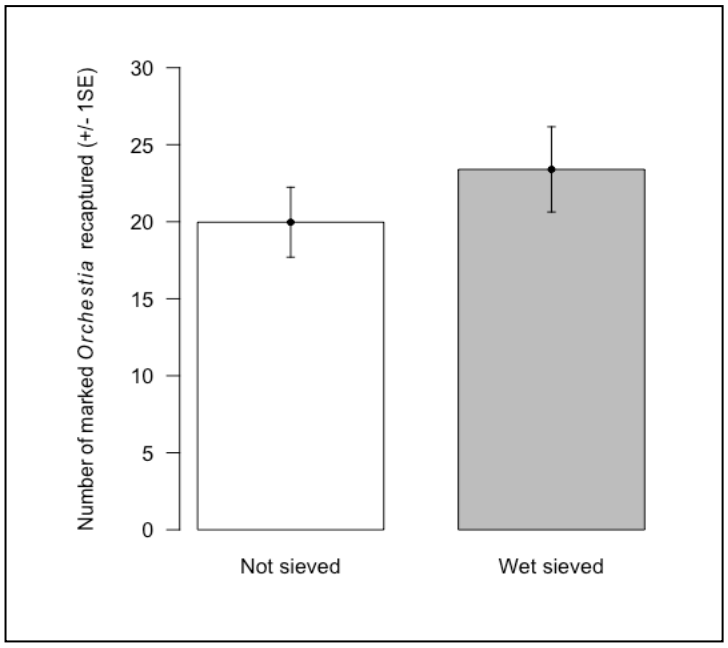


Figure 2.5 *The only significant variable from Table 2.3 – wet sieved samples when compared to samples not sieved.*

The main mark-recapture experiment was then conducted to evaluate if *Orchestia* move through their own means without tidal influence, and if they are displaced by tidal ebb and flow. Forty-two 20cm x 20cm plots were chosen in *Orchestia* habitat. Twenty-one were control plots, covered by plastic containers that allowed air and seawater ingress, but prevented *Orchestia* escaping, and held in place by netting and pegs, whilst 21 were left exposed. *Orchestia* were collected and marked in situ with a small spot on their thorax of quick-drying fluorescent varnish, before being returned to their original position. The plots, control and exposed, received one of two treatments; they were either left in place over two high tides, or had no tidal coverage. Upon revisit the 20m x 20m turve was removed from the plot and taken away to count the remaining marked *Orchestia*. The number of marked *Orchestia* recaptured was normally distributed, showed no collinearity between predictor variables and was therefore modelled using a linear model.

Prey depression experiment

Objective 12 hypothesised that redshanks feeding in an area would depress *Orchestia* numbers which would then move into the subsoil before moving back to the surface later. This experiment was conducted in winter 2 between 13 Jan 2015 and 4 Mar 2015. Twenty-six plots were chosen in the centre of redshank feeding flocks and counts taken immediately after they had flown off. As above, redshanks had been foraging in these areas from between 5 and 40 minutes. A 1m x 1m quadrat was used to count surface *Orchestia*. The plot was marked at each corner to record its position, and was revisited for a second count between 24 and 48hrs later, before any tidal coverage. *Orchestia* were removed for identification, sizing and sexing. *Orchestia* found were compared against first count and second count, for each species separately and together. In this instance, for each model a poisson GLM was used initially, but this showed an overdispersion parameter value of >5 for each set of models. To correct this the procedure is to use a quasi-poisson GLM which reduces the standard errors (Thomas *et al*., 2015). Here the variance was theta*mu, where mu equalled the mean of the distribution of the response variable and theta was the

dispersion parameter of the quasi-poisson GLM (Thomas *et al*., 2015).

The effect of weather on Orchestia movement

Objective 13, the final one of this chapter, predicted that *Orchestia* will jump and crawl more and quicker, in warmer temperatures. When disturbed *Orchestia* react either by remaining curled up and quiescent, or they crawl a short distance, jump several times and then crawl into the soil (pers. obs.). They were categorised as inactive, when they could be touched with the blade of a penknife without moving, or jumping. One hundred and twenty samples were taken in winter 3 between 11 Nov 2015 and 21 Mar 2016, both from the surface using the 1m x 1m quadrat, and subsurface using the 10cm x 10cm quadrat placed in the centre. Soil was taken out of this quadrat down to a depth of 6cm and *Orchesti*a activity behaviour recorded. The weather variables, air temperature, soil temperature and wind speed were measured as per the distribution sampling experiment above. Models were constructed for four categories: surface inactive and surface jumping, and subsurface inactive and subsurface jumping. No identification was possible because the species could not be distinguished without being captured.

For analyses, first, GLMMs from the lme4 package (Bates *et al*., 2015) were used, and day number was entered as a random effect, using a poisson distribution. However, there was very little variance or no variance at all explained by the random factor, so for the surface inactive and subsurface models, poisson GLMs were used due to zero inflation. For the surface active model, overdispersion was present with a parameter value of 2.8 so a quasi-poisson GLM was used instead in accordance with Thomas *et al*. (2015). Thirty-two additional plots were visited in redshank feeding areas to determine *Orchestia* speed of movement. This was assessed as slow or quick. *Orchestia* that did not move or crawled sluggishly were categorised as slow, whereas those making a concerted means to escape by crawling quickly or jumping were categorised as quick. The 1m x 1m quadrat was used and again individuals were not captured, so no identification was made of the species. GLMMs were constructed for each category using the lme4 package (Bates *et al*., 2015) as above, where plot serial number was entered as a random factor, to quantify the amount of the variance when tested.

2.3 Results

2.3.1 Size and composition of *Orchestia*

Size of Orchestia – objective 1

In total 4398 *Orchestia* were identified, sized and sexed during the research. A breakdown of numbers is given in Table 2.4.

Table 2.4 *Numbers of Orchestia removed for identification, sizing and sexing for objectives 1 and 2.*

Species	Winter 1 numbers	Winter 2 numbers	Winter 3 numbers		Total for each species
O. gammarellus					
Male	169	242	331		
Female	260	409	504		
Juvenile <8mm	106	203	224		
Total	535	854	1059		2448
O. mediterranea					
Male	337	191	137		
Female	387	274	245		
Juvenile <8mm	137	145	97		
Total	861	610	479		1950
Total for winter	1396	1464	1538	Grand total	4398

Table 2.5 *Size of Orchestia against species, sex and year – gaussian GLM.*

Variable	Estimate	SE	*z*	*P*
Intercept	6.57	0.14	45.9	**<0.001**
O. mediterranea	0.09	0.13	0.7	0.486
Male	4.86	0.18	26.8	**<0.001**
Female	3.58	0.17	21.1	**<0.001**
Winter 2	- 0.05	0.16	-0.3	0.743
Winter 3	-0.12	0.16	-0.7	0.464
Male*winter 2	-0.76	0.20	-3.7	**<0.001**
Female*winter 2	-0.18	0.19	-0.9	0.341
Male*winter 3	-0.02	0.21	-0.1	0.937
Female*winter 3	0.33	0.20	1.7	0.091
*O. mediterranea**male	-1.12	0.17	-6.6	**<0.001**
*O. mediterranea**female	-0.47	0.16	-3.0	**0.002**

Significant *P* values are marked in bold. Intercept includes *O. gammarellus*, juveniles, and winter 1 categorical variables. The Pseudo-R^2 (explained deviance) for this model is 0.41. Degrees of freedom 4385. Best model AIC: 18176, full model AIC: 18180. Variables removed from full model: *Orchestia* species*winter.

The maximum *O. gammarellus* individual was 19mm (male) and the minimum 3mm. This was 18mm (male) and 3.5mm for *O. mediterranea*. The largest *O. gammarellus* female was 17.5mm and *O. mediterranea* female 18 mm, the same size as the male. The data were entered into a Gaussian GLM where size was measured against

winter, sex and species. Males of both species were significantly larger than females, although for *O. mediterranea* the difference in size was less and ranged between 0.6, 0.1 and 0.3mm for winters 1 to 3 respectively. For *O. gammarellus* this was 1.7, 0.7 and 0.9mm. Therefore, the objective 1 hypothesis that the sexes of *Orchestia* are sexually dimorphic, with males being larger than females, is proven. In addition, *O. mediterranea* males were significantly smaller than *O. gammarellus* males by 1mm for each of the three winters. Although *O. mediterranea* females were closer in size to *O. gammarellus* females, they were nevertheless slightly smaller by 0.3, 0.3 and 0.4 mm respectively in winters 1 to 3. Males of both species of *Orchestia* were significantly smaller in winter 2 when compared to the other winters (Table 2.5, Figure 2.6). The majority of results from the Tukey post-hoc test to compare multiple comparisons of means were significantly different, except (1) juveniles of both species were not significantly different across winters, (2) *O. gammarellus* females and *O. mediterranea* males were not significantly different in size (Figure 2.6).

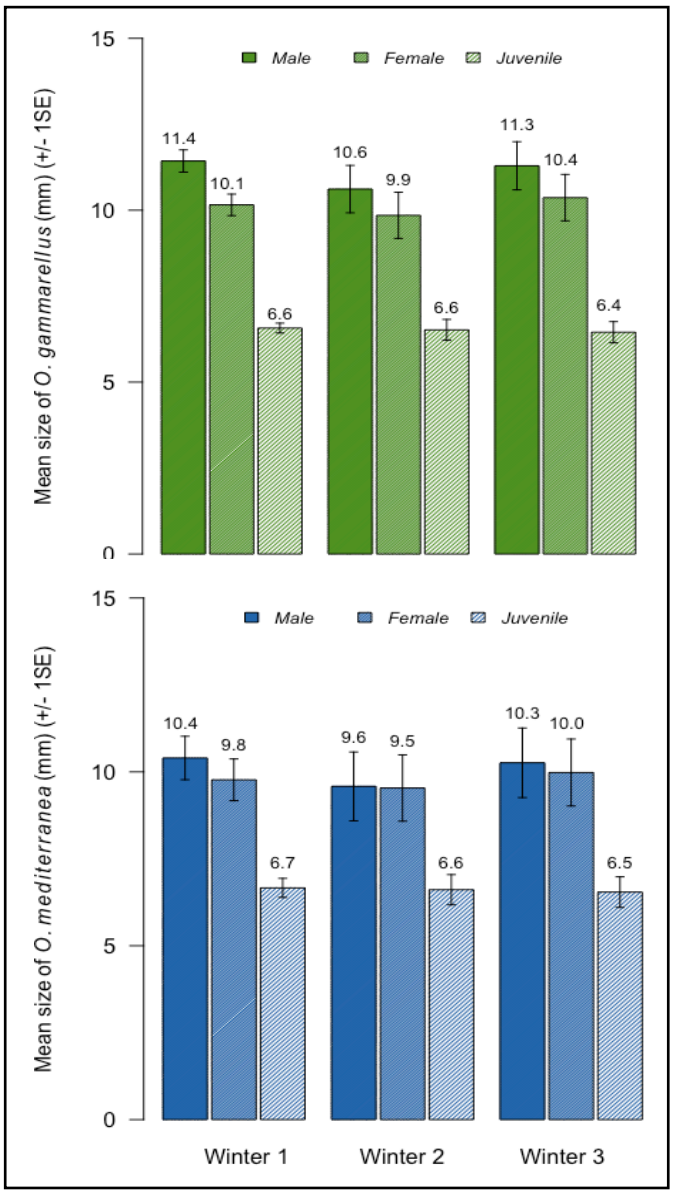


Figure 2.6 *Mean sizes of Male, female and juvenile O. gammarellus (top) and O. mediterranea (bottom). Winters 1, 2 and 3. Parameter estimates and SEs plotted from the model in Table 2.5.*

Composition of the Orchestia populations – objective 2

The *Orchestia* data that were used for this objective are detailed in Table 2.3. When males and females were compared to assess the make-up of the adult population across winters 1, 2 and 3 the results indicated that there were more females than males for both *O. gammarellus* and *O. mediterranea* (Figure 2.7). Chi-squared tests for *O. gammarellus* showed no significant difference between male and female composition ($\chi^2(2, n = 1915) = 1.03$, $p = 0.60$) across the three winters, where females made up around two thirds of the adult population (Figure 2.7). *O. mediterranea* composition was more evenly balanced between males and females in winter 1 (almost 50:50), but in winter 2 females made up slightly less than three fifths, and slightly more than three fifths in winter 3. Chi-squared tests showed that for *O. mediterranea* there was a significant difference in the composition of adults across the 3 winters ($\chi^2(2, n = 1351) = 12.1$, $p < 0.01$), but when winter 3 was excluded, winters 1 and 2 resulted in no significant difference between male and female composition, although this was marginal ($\chi^2(2, n = 1189) = 3.2$, $p = 0.07$). (Figure 2.7).

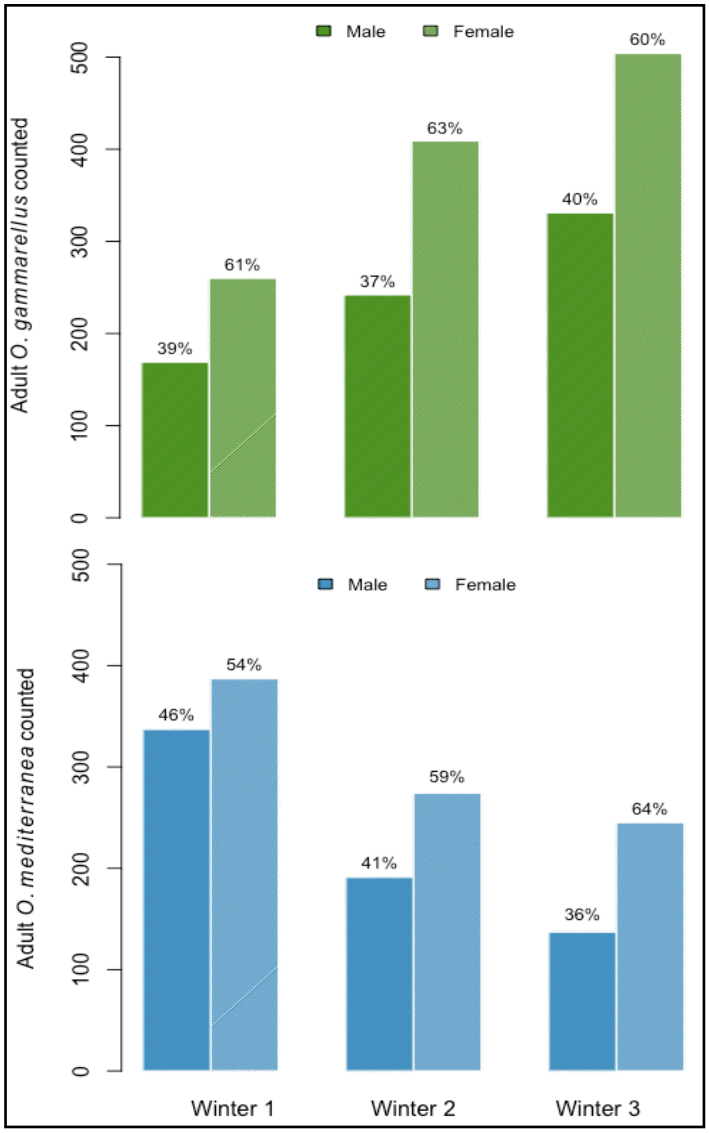


Figure 2.7 *The composition of male and female Orchestia over winters 1, 2 and 3. O. gammarellus (top), O. mediterranea (bottom).*

When the proportion of adults to juveniles was compared across all winters, juveniles accounted around a fifth of the population for each species of *Orchestia*. For *O. gammarellus* there was no significant difference in this composition when tested with chi-squared (Pearson's) ($\chi^2(2, n = 2448) = 3.4, p = 0.18$). However, *O. mediterranea* did show a significant difference between the three winters ($\chi^2(2, n = 1950) = 14.3, p < 0.001$), but it was the difference between winters 1 and 2 which influenced this ($\chi^2(1, n = 1471) = 13.7, p < 0.001$), because there was no significant difference between winters 1 and 3 ($\chi^2(1, n = 1340) = 3.7, p < 0.053$) (marginal) and 2 and 3 ($\chi^2(1, n = 1089) = 1.72, p < 0.19$) (Figure 2.8).

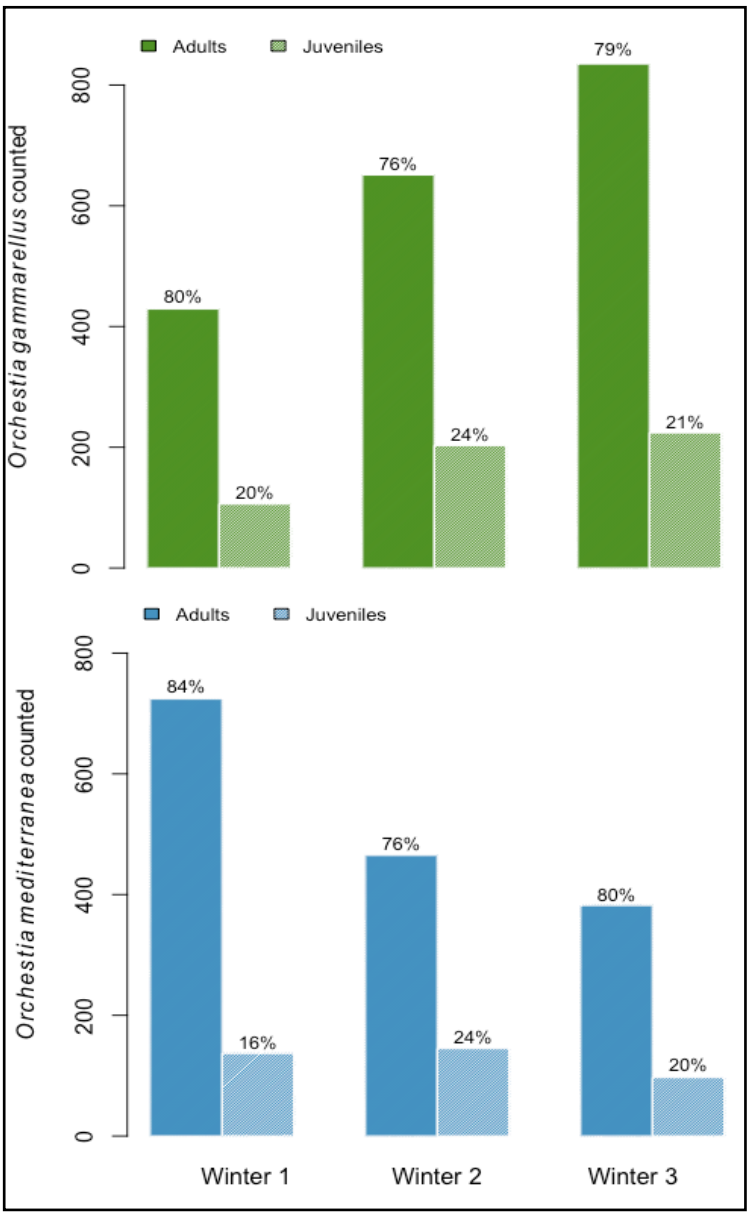


Figure 2.8 *The composition of adult and juvenile Orchestia over winters 1, 2 and 3. O. gammarellus (top, O. mediterranea (bottom.*

Size of Orchestia in redshank feeding and non-feeding areas – objective 3

In winters 2 and 3, 328 plots were visited in feeding and non-feeding areas and 2098 *Orchestia* taken for identification, and sizing (Table 2.6). The best GLMMs for *O. gammarellus* showed that there was no significant

difference in size between redshank feeding and non-feeding areas. The best GLMM for *O. mediterranea* showed that the mean size of individuals in winter 2 was 1.1mm smaller in non-feeding areas compared to feeding areas. However, this contrasted with winter 3 where *O. mediterranea* were 0.3mm larger in non-feeding areas (Table 2.7, Figure 2.9).

Table 2.6 *Number of plots and numbers of Orchestia removed for identification, sizing and sexing across winters 2 and 3. Objective 3 – size of Orchestia in redshank feeding and non-feeding areas*

Plots	Winter	Number of plots
Redshank feeding area	2	48
	3	60
	Total	108
Redshank non-feeding area	2	146
	3	74
	Total	220
	Grand total	328

Orchestia	Species	Winter	Number of *Orchestia*
	O. gammarellus	2	854
		3	1010
		Total	964
	O. mediterranea	2	611
		3	477
		Total	1088
		Grand total	2098

Table 2.7 *Best GLMM for O. mediterranea size from redshank feeding and non-feeding areas, comparing winters 2 and 3, where the plot number was entered as a random effect.*

Variable	Estimate	SE	*t*	*P*
Intercept	9.65	0.25	38.84	**0.001**
Non-feeding area	-1.09	0.29	-3.80	**<0.001**
Winter 3	-0.46	0.39	-1.19	0.237
Non-feeding area*Winter 3	1.40	0.45	3.01	**0.002**

Significant *P* values are marked in bold. Degrees of freedom 1084. Variance of fixed effects = 0.17, variance by random effects = 0.05. Plot number entered in the model as a random effect.

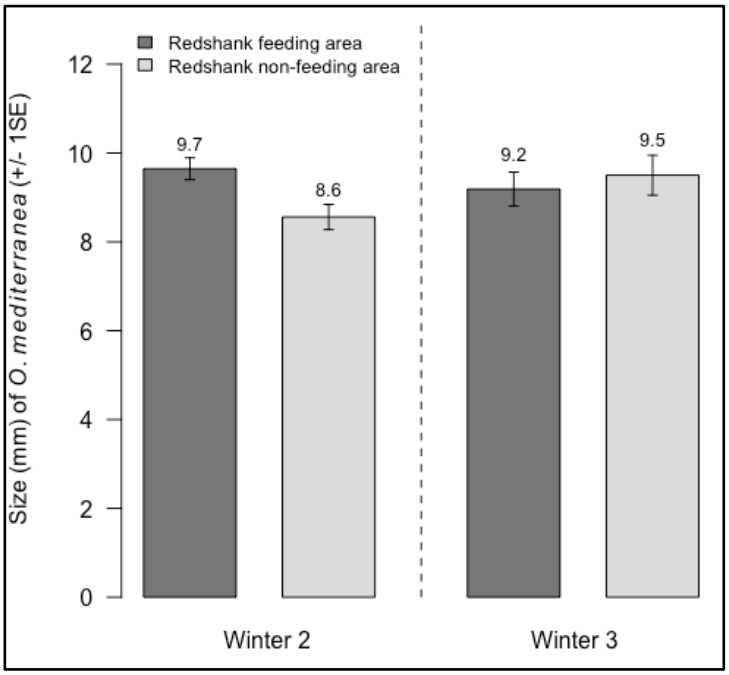


Figure 2.9 *Size of O. mediterranea between redshank feeding and non-feeding areas in winter 2 (left) and winter 3 (right). O. mediterranea were measured from randomly selected non-feeding areas and from areas where redshanks were seen feeding. O. mediterranea were larger in feeding areas in winter 2, but smaller in winter 3. Parameter estimates and SEs plotted from the model in Table 2.7.*

Size of Orchestia when feeding plots were revisited – objective 4

The recorded data for this objective are in Table 2.8. This shows numbers of *Orchestia* means and SEs for the predictor variables used in the multivariate models.

Table 2.8 *Number, mean size and SE for Orchestia from 26 redshank feeding plots for 1st and 2nd visits.*

Type of data	1st visit			2nd visit		
	N	Mean size (mm)	SE	*N*	Mean size (mm)	SE
All Orchestia	196	9.44	0.15	140	9.25	0.21
O. gammarellus	124	9.47	0.20	76	8.91	0.30
O. mediterranea	72	9.38	0.21	64	9.66	0.27

In winter 2, when redshank feeding plots were revisited between 1 and 6 days later, there was no significant effect for size difference of *Orchestia* between the first and second visit. This was the case for all *Orchestia* (est -0.01, SE 0.02, t -0.56, $P = 0.57$, $n = 335$) and when each species was tested separately (*O. gammarellus*: est = -0.02, SE = 0.04, $t = -0.40$, $P = 0.69$, $n = 95$; *O. mediterranea:* est = -0.01, SE = 0.03, $t = -0.10$, $P = 0.92$, $n = 180$).

2.3.2 Distribution of *Orchestia* – objectives 5-10

A breakdown of the data collected for this part of the research is illustrated in Table 2.9a and 2.9b. This shows numbers of *Orchestia* means and SEs for the predictor variables used in the multivariate models.

Table 2.9 *The data for Orchestia counts in winter 1. a. Orchestia numbers, means and SEs against each predictor and, b. Predictor means and SEs for each Orchestia species when present.*

a.

Predictor variable		*O. gammarellus*			*O. mediterranea*		
High tide area	High tide height	*N*	Mean	SE	*N*	Mean	SE
1	> 5.6	41	0.55	0.30	19	0.26	0.10
2	5.5 – 5.59	61	4.36	2.40	2	0.14	0.10
3	5.4 – 5.49	47	5.22	5.63	0	0.00	0.00
4	5.3 – 5.39	54	9.00	8.60	2	0.33	0.33
5	5.2 – 5.29	175	1.94	0.34	38	0.42	0.12
6	5.1 – 5.19	62	1.27	0.44	33	0.67	0.33
7	5.0 – 5.09	22	0.61	0.19	66	1.83	0.67
8	4.9 – 4.99	14	0.82	0.51	17	1.00	0.34
9	4.8 – 4.89	94	0.44	0.10	613	2.85	0.30
10	4.7 – 4.79	1	0.03	0.03	74	2.06	0.56
11	4.6 – 4.69	0	0.00	0.00	16	0.84	0.55
12	4.5 – 4.59	2	0.17	0.17	3	0.25	0.13
13	< 4.5	41	0.34	0.13	22	0.18	0.07
P. maritima		323	3.14	0.35	829	4.34	0.32
F. rubra		221	7.89	2.14	28	3.11	0.65
S. europaea		6	1.50	0.29	90	3.60	0.77
A. maritima		152	2.58	0.26	171	3.56	0.59
S. maritima		218	2.79	0.35	803	4.59	0.34
A. tripolium		139	2.78	0.42	523	4.80	0.40
Pl. maritima		230	3.38	0.44	158	3.22	0.38

b.

Predictor variable	*When O. gammarellus is present*		*When O. mediterranea is present*	
	Mean	SE	Mean	SE
Vegetation density (%)	84.43	1.56	79.40	1.21
Vegetation height (mm)	66.46	3.32	69.67	2.15
P. maritima (%)	28.67	2.21	38.25	1.51
F. rubra (%)	13.90	2.49	2.94	1.04
S. europaea (%)	0.17	0.12	1.13	0.31
A. maritima (%)	13.61	1.86	5.45	0.98
S. maritima (%)	4.16	0.49	7.52	0.49
A. tripolium (%)	1.05	0.17	1.69	0.16
Pl. maritima (%)	3.12	0.39	1.99	0.33
Elevation (m)	3.79	0.08	3.80	0.07
Distance from nearest creek edge (m)	13.80	3.46	7.14	1.28

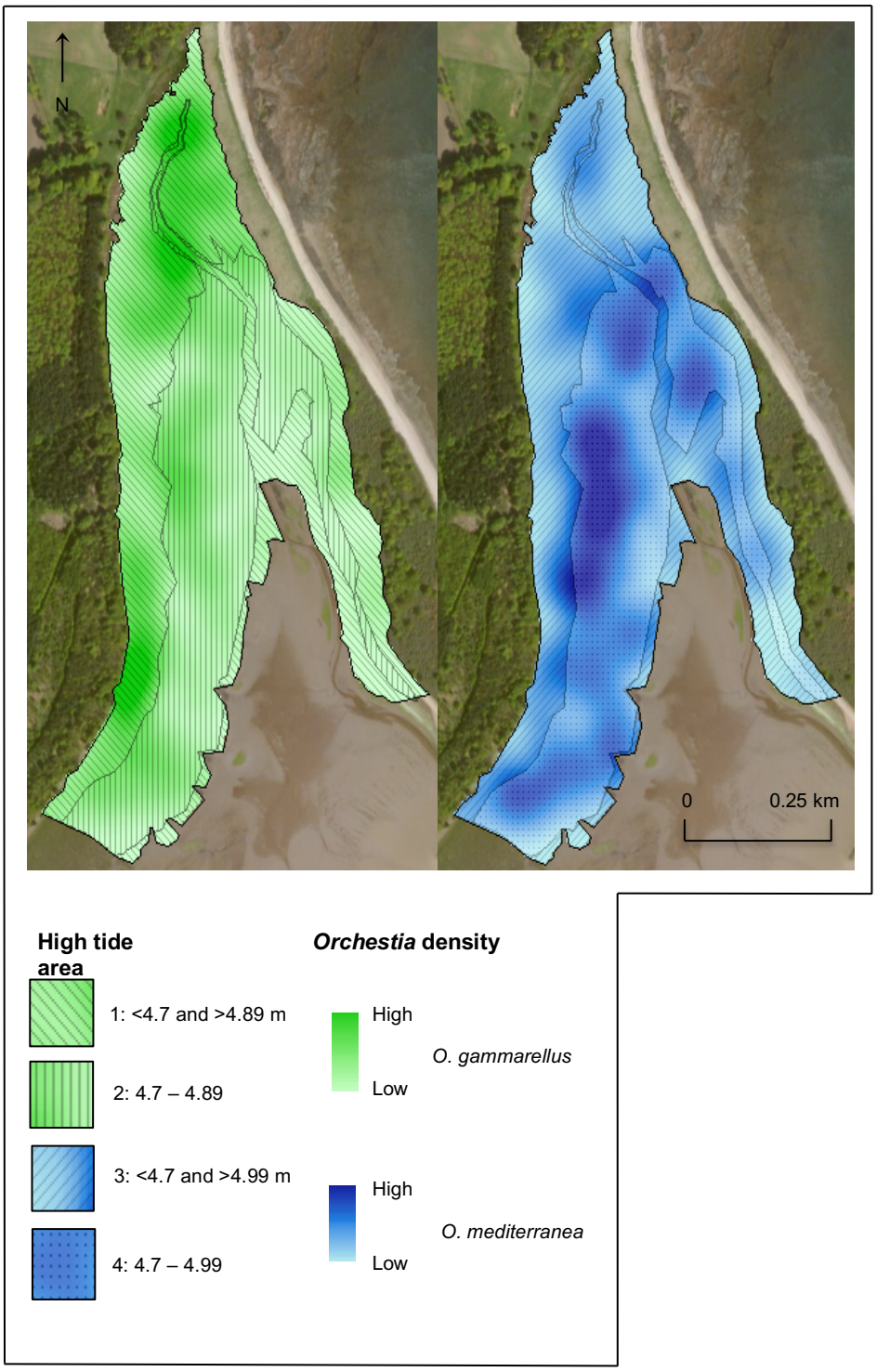


Figure 2.10 *Density gradient maps and high tide area designations and their coverage, from the best binomial GLM for each Orchestia species. The original 13 categorical levels of high tide were combined into two levels for each species, 1 and 2 for O. gammarellus and 3 and 4 for O. mediterranea. The high tide area designations were very similar for each species although occurrence in these areas produced contrasting results (Table 2.10 and 2.11).*

Presence/absence

Initial investigation of *Orchestia* distribution was carried out using ArcGIS software (ESRI, 2013), where digital visualisation of presence and absence data showed the areas where each *Orchestia* species was most likely to occur. The densest occurrence of *O. gammarellus* was in the north of the saltmarsh and in an area adjacent to the

south west perimeter. *O. mediterranea* was concentrated mainly on the western mid-marsh, but also at lesser densities in three areas to the north east and the south west (Figure 2.10). Multivariate models containing predictor variables applicable to objectives 5 – 10 were then be built for each species (Table 2.10 for *O. gammarellus* and Table 2.11 for *O. mediterranea*).

Table 2.10 *O. gammarellus distribution – presence probability - best binomial GLM.*

Variable	Estimate (Log)	SE(Log)	*z*	*P*
Intercept	-2.27	0.59	-3.8	**<0.001**
F. rubra	0.03	0.08	3.8	**<0.001**
S. europaea	-0.01	0.07	-1.7	0.079
Day number	-0.01	0.01	-2.3	**0.020**
Distance from nearest creek edge	0.01	0.01	0.1	0.876
Vegetation density	0.03	0.01	4.3	**<0.001**
High tide area 2 (4.7m - 4.89m)	-1.03	0.23	-4.3	**<0.001**
Distance from nearest creek edge*Vegetation density	-0.01	0.01	-2.6	**0.009**

Significant *P* values are marked in bold. Intercept includes categorical tidal level *High tide area 1 (<4.7m, >4.89m)*. The Pseudo-R^2 (explained deviance) for this model is 0.18. Degrees of freedom 505. Best model AIC: 507, full model AIC: 521. Variables removed from full model: *S. maritima*, *P. maritima*, *Pl. maritima*, *A. tripolium*, *A. maritima*, day number^2, vegetation height, elevation, days to/from nearest Spring tide.

Table 2.11 *O. mediterranea distribution – presence probability - best binomial GLM.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	-0.72	0.43	-1.7	0.092
A. maritima	-0.03	0.01	-4.4	**<0.001**
S. europaea	0.04	0.02	2.2	**0.027**
A. tripolium	0.16	0.07	2.2	**0.030**
Distance from nearest creek edge	- 0.02	0.01	-3.2	**<0.001**
High tide area 4 (4.7m – 4.99m)	1.01	0.25	-4.1	**<0.001**
Vegetation density	0.01	0.01	2.7	**0.006**
*S. maritima***A. tripolium*	0.01	0.01	-1.9	0.066

Significant *P* values are marked in bold. Intercept includes categorical tidal level, *High tide area 3 (<4.7m, >4.99m)*. The Pseudo-R^2 (explained deviance) for this model is 0.23. Degrees of freedom 501. Best model AIC: 541, full model AIC: 558. Variables removed from full model: *F. rubra*, *F. rubra*^{2}, *P. maritima*, *Pl. maritima*, *S. europaea*, day number, day number^2, elevation, vegetation height, *F. rubra***A. maritima*, *P. maritima***A. tripolium*, high tide area*distance from the nearest creek edge, *F. rubra**distance from the nearest creek edge.

Abundance

Similarly, models were developed for *Orchestia* abundance containing predictor variables relative to the same objectives (5-10), the results of which are shown in Tables 2.12 (*O. gammarellus*) and 2.13 (*O. mediterranea*).

Table 2.12 *O. gammarellus distribution – abundance - best poisson GLM*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	1.35	0.26	5.1	**<0.001**
F. rubra	0.02	0.01	2.1	**0.038**
F. rubra^2	-0.01	0.01	-3.4	**<0.001**
A. maritima	-0.01	0.01	-4.6	**<0.001**
P. maritima	-0.01	0.01	-3.2	**<0.001**
S. maritima	-0.08	0.01	-6.1	**0.001**
Pl. maritima	-0.06	0.01	-5.2	**<0.001**
A. tripolium	-0.18	0.04	-4.7	**<0.001**
Distance from nearest creek edge	-0.01	0.01	-2.3	**0.002**
Vegetation density	0.01	0.01	3.4	**<0.001**
*F. rubra*A. maritima*	0.01	0.01	2.2	**0.024**
*S. maritima*A. tripolium*	0.02	0.01	5.3	**<0.001**

All P values significant. The Pseudo-R^2 (explained deviance) for this model is 0.27. Degrees of freedom 129. Best model AIC: 727, full model AIC: 771. Variables removed from full model: *S. europaea*, day number, day number^2, vegetation height, elevation, high tides per annum, high tides per annum^2, *A. maritima*P. maritima*, *S. maritima* P. maritima*, *A. tripolium*P. maritima*, S. *maritima*S. europaea*, *F. rubra**distance to nearest creek edge, *F. rubra*^{2}*distance to nearest creek edge, *F. rubra**elevation, *F. rubra*^{2}*elevation, *F. rubra*Pl. maritima* distance to nearest creek edge*elevation, distance to nearest creek edge*vegetation density, distance to nearest creek edge*high tides per annum.

Table 2.13 *O. mediterranea distribution – abundance - best poisson GLM.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	1.51	0.26	.5.7	**<0.001**
F. rubra	-0.01	0.01	-3.2	**<0.001**
A. maritima	-0.02	0.01	-3.3	**<0.001**
P. maritima	-0.01	0.01	-3.3	**<0.001**
S. europaea	-0.04	0.01	-3.9	**0.015**
Day number	-0.03	0.01	-0.8	0.439
Day number^2	0.01	0.01	2.1	**0.038**
Distance from nearest creek edge	-0.01	0.01	-2.2	**0.026**
High tide area	0.01	0.01	2.1	**0.034**
High tide area^2	-0.01	0.01	-3.1	**0.002**
*A. maritima *P. maritima*	-0.01	0.01	-2.7	**0.006**

Significant P values marked in bold. The Pseudo-R^2 (explained deviance) for this model is 0.22. Degrees of freedom 193. Best model AIC: 1160, full model AIC: 1170. Variables removed from full model: *F. rubra*^{2}, *S. maritima*, elevation, days to/from nearest Spring tide, *S. maritima*P. maritima*, *S. maritima*S. europaea*, distance from nearest creek edge*elevation, distance from nearest creek edge*days to/from nearest Spring tide, *F. rubra**elevation, *F. rubra*^{2}*elevation.

Tidal coverage and its effect on Orchestia distribution – objective 5

Orchestia presence

When tidal coverage was entered into presence/absence models, the probability that *O. gammarellus* occurred in high tide area 1 was 0.38 compared to high tide area 2 which was 0.18. Hence, *O. gammarellus* was more likely to be found in low marsh high tides (<4.7m) and outer marsh high tides (>4.89m). They were less likely to occur in the mid-marsh area between high tides of 4.7 and 4.89m (Table 2.10, Figure 2.12).

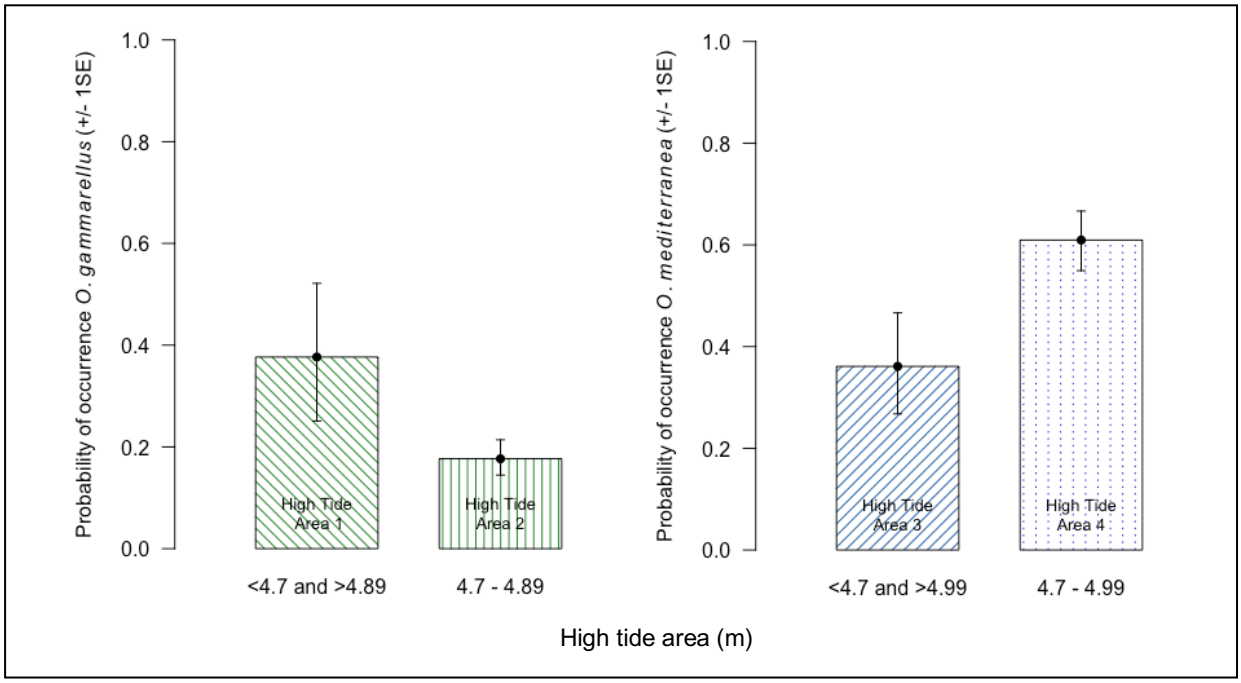


Figure 2.11 *High tide area and the probability of occurrence of each species of Orchestia. The categorical variable high tide area was reduced from 13 levels to 2 per species, which gave the most parsimonious models. Parameter estimates and SEs plotted from the model in Tables 2.10 and 2.11.*

The probability of occurrence of *O. mediterranea* in high tide area 3 (<4.7m and >4.99m) was 0.36, increasing to 0.61 in high tide area 4 (4.7m – 4.99m) (Table 2.11, Figure 2.11). They are therefore more likely to be present in the mid marsh compared to the outer and inner marsh areas.

Orchestia abundance

High tide area was dropped from the best *O. gammarellus* model where it was entered as a continuous variable because it had no significant effect (Table 2.12).

For *O. mediterranea,* high tide area produced poorer models when tide was entered as a categorical variable even though various combinations of levels were tried. Therefore, high tide was entered as a continuous variable – *number of high tides per annum*, and in the best poisson GLM, the quadratic of this variable was also entered and showed a significant effect. A positive quadratic regression indicated a small increase in abundance from 3.7 individuals in the outer saltmarsh (0 high tides per annum), to 5.2 individuals near the centre (280 high tides per

annum), down to 1.8 individuals in the inner marsh which receives 700 high tides per annum (Table 2.13, Figure 2.12).

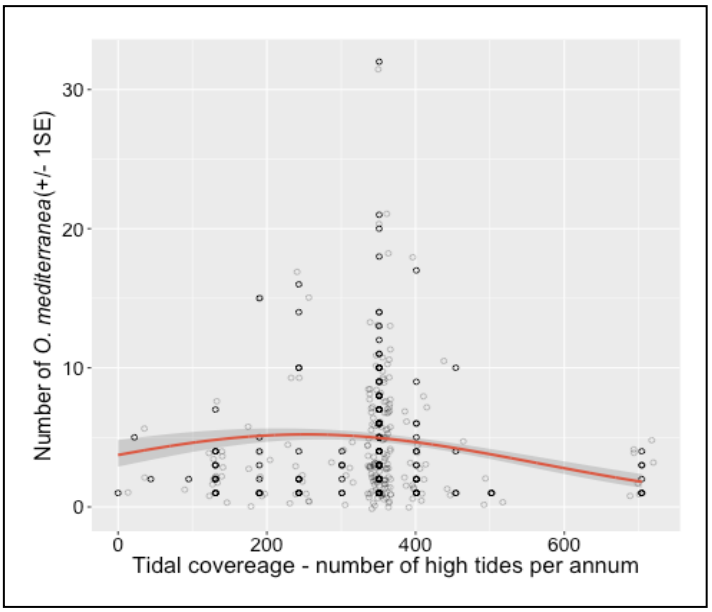


Figure 2.12 *The relationship between high tide and abundance for O. mediterranea abundance where high tide was a continuous variable consisting of number of high tides per annum that covered the sample plot and which shows a positive quadratic effect. The darker the point, the more measurements at that reading. Jittering was used to disperse these points for clarity. Parameter estimates and SEs plotted from the model in Table 2.13.*

Distance from the nearest creek edge – objective 6

All the best models resulted in a negative relationship between *Orchestia* and distance from the creek edge. For *O. gammarellus*, the best binomial GLM showed that distance from the nearest creek edge had no significant effect as a single predictor variable but was significant as an interaction with overall vegetation density. For high tide areas 1 and 2, at maximum vegetation density, the probability of *O. gammarellus* being present decreased from 0.65 and 0.40 to almost zero respectively between a minimum distance of 6cm and a maximum of 455m from the creek edge. At median vegetation density, this was a probability of 0.52 for high tide area 1 and 0.27 for high tide area 2 down to almost zero over the same distance range. However, in contrast there was a slight increase when overall vegetation density was at a minimum for the same distances. For high tide area 1 the probability of being present was 0.10 to 0.12, and for high tide area 2, 0.06 to 0.07 (Table 2.10, Figure 2.13). The best poisson GLM for *O. gammarellus* showed that abundance decreased from 7.8 individuals to less than 1, between 10cm and 455m distance from the creek edge (Table 2.12, Figure 2.13).

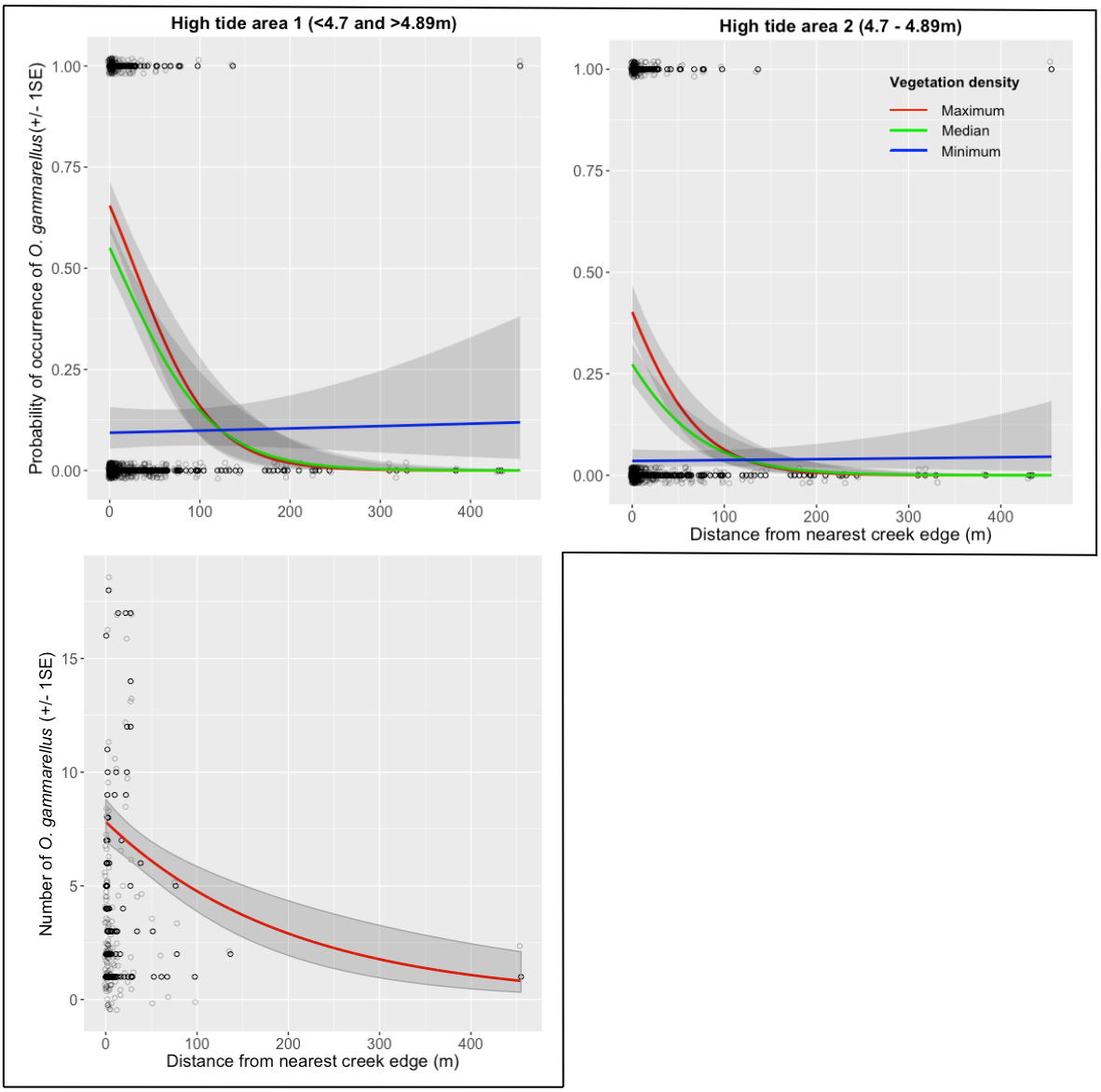


Figure 2.13 *Top left and right - Distance from the nearest creek edge and its relationship and the probability of occurrence of O. gammarellus. Only the interaction with overall vegetation density showed a significant effect. This resulted in a negative relationship for maximum and median overall vegetation densities and a slight positive effect for minimum overall vegetation density. This was the case for both high tide areas 1 and 2. Bottom left – the abundance of O. gammarellus and distance from the nearest creek edge. The darker the point, the more measurements at that reading. Jittering was used to disperse some of these points (Tables 2.10, 2.12).*

The best binomial GLM for *O. mediterranea* also resulted in a decrease in presence as distance from the creek edge increased, from a probability of 0.38 (high tide area 3) and 0.63 (high tide area 4) at a minimum of 6cm away down to almost zero at 455m maximum distance the nearest creek edge (Table 2.11, Figure 2.14). The decrease in the best abundance model for *O. mediterranea* was from 5 individuals at 6cm to just over one at 228m distance from the creek edge (Table 2.13, Figure 2.14).

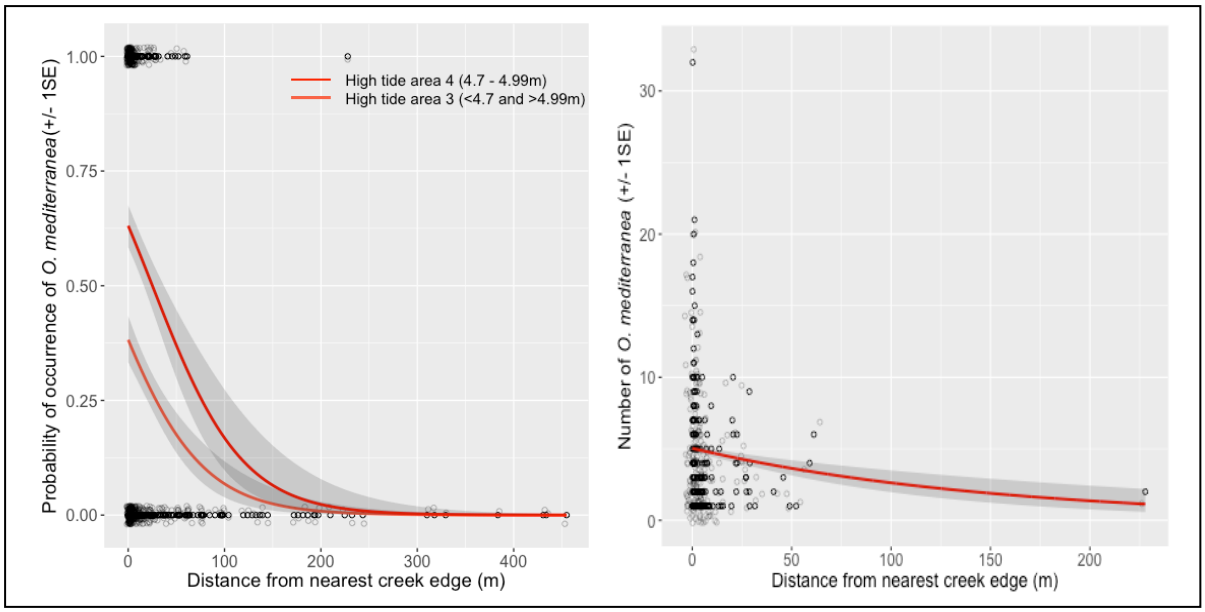


Figure 2.14 *Left – The probability of occurrence of O. mediterranea showed a negative relationship for high tide areas 3 and 4, where the probability decreased as distance from the creek edge increased. Right – the abundance plot for the same species showed a negative relationship where O. mediterranea decreased in numbers the further from the nearest creek edge. The darker the point, the more measurements at that reading. Jittering was used to disperse these points Parameter estimates and SEs plotted from the model in Tables 2.11 and 2.13.*

Seasonal effect – objective 7

The effect of the overwinter period on *O. gammarellus* presence showed a negative effect in the best binomial GLM for the two categorical levels of tide. Thus, for high tide area 1 the probability of occurrence reduced from 0.52 on day 1 of the study period (10 Nov 2013) to 0.31 on the last day - 135 (24 Mar 2014). For high tide area 2 this was 0.28 to 0.14 across the same period (Table 2.10, Figure 2.15). Overwinter period was dropped from the best binomial GLM for *O. mediterranea*.

Seasonal effect of the overwinter period was also dropped from the best poisson GLM for *O. gammarellus* and the best binomial GLM for *O. mediterranea*, whereas the best poisson GLM for *O. mediterranea* showed that although overwinter period had no significant effect, it did when entered as a quadratic variable. When the estimates were compared between the models with and without the quadratic variable, although AIC values were very similar (AIC:1159.9 – simpler model without quadratic, AIC:1161.9 – more complex model with quadratic), the more complex model was used as the best model (likelihood ratio test: χ^2=4.3, *P*=0.04). The model showed a negative quadratic effect where there was a slight decrease in abundance at day 1 of 4.6 individuals down to 4.5 at day 50 (2nd week in Jan 2014), before an increase of 7.9 at day 135 (Table 2.13, Figure 2.15).

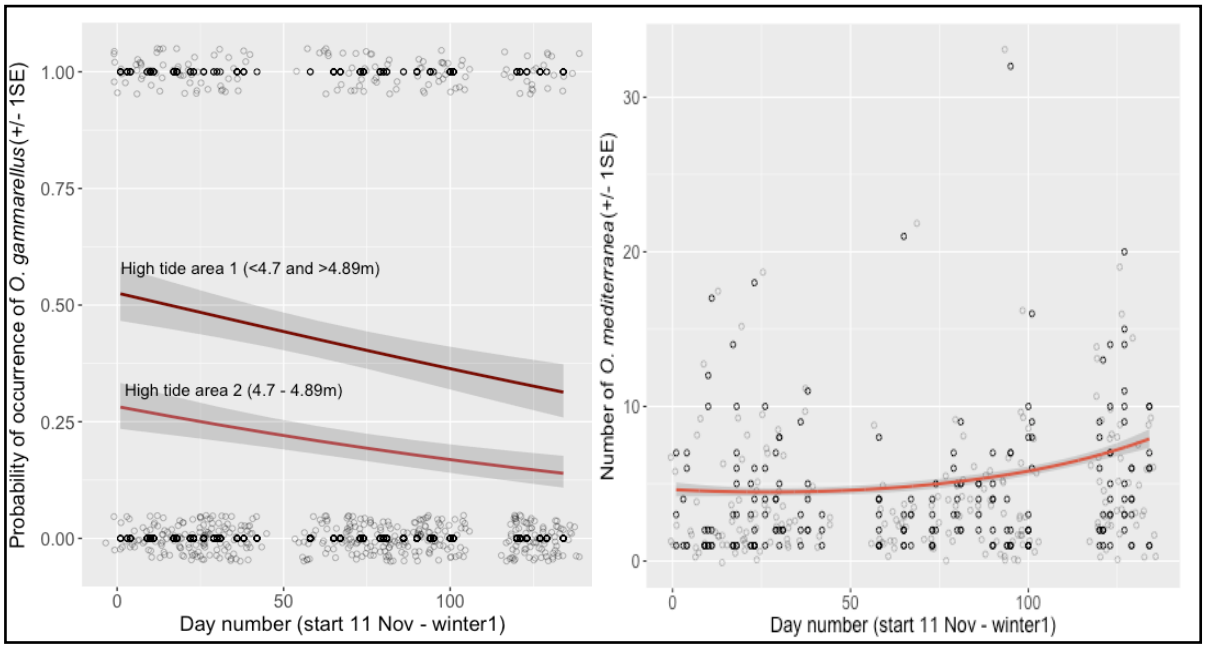


Figure 2.15 *The seasonal effect on the probability and abundance of Orchestia in winter 1. Day 1 was 11 Nov 2013 and the last day (135) was 24 Mar 2014. Left – O. gammarellus and the probability of occurrence for high tide areas 1 and 2, which shows a negative relationship, where the probability of occurrence decreases through the period. Right – the abundance of O. mediterranea shows a negative quadratic effect where abundance dips slightly (barely noticeable and of little biological significance), before increasing as the winter progresses. The darker the point, the more measurements at that reading. Jittering was used to disperse these points. Parameter estimates and SEs plotted from the model in Tables 2.10 and 2.13 refer.*

Vegetation coverage and Orchestia distribution – objectives 8 and 9

Orchestia presence and vegetation

Only one species of vegetation showed a significant effect in the best binomial GLM for the probability of *O. gammarellus* occurrence and that was *F. rubra,* where the probability of occurrence increased by a factor of 2.4 from 0% to 90% (max) plant density for both tidal areas. *S. europaea* showed a marginal non-significant effect where the probability of *O. Gammarellus* occurrence decreased from 0.38 (high tide area 1) and 0.18 (high tide area 2) where there was no *S. europaea* present, to almost zero probability at 40% (max) *S. europaea* coverage (Table 2.10, Figure 2.16). Therefore, *O. gammarellus* prefers *F. rubra*, a species associated with the outer saltmarsh, compared to *S. europaea* an inner marsh species.

Overall vegetation density of the sample plot showed that the probability of *O. gammarellus* occurrence increased from 0.02 to 0.51 and 0.06 to 0.27 for high tide areas 1 and 2 respectively, where vegetation densities ranged from zero to 100% coverage (Table 2.10, Figure 2.16).

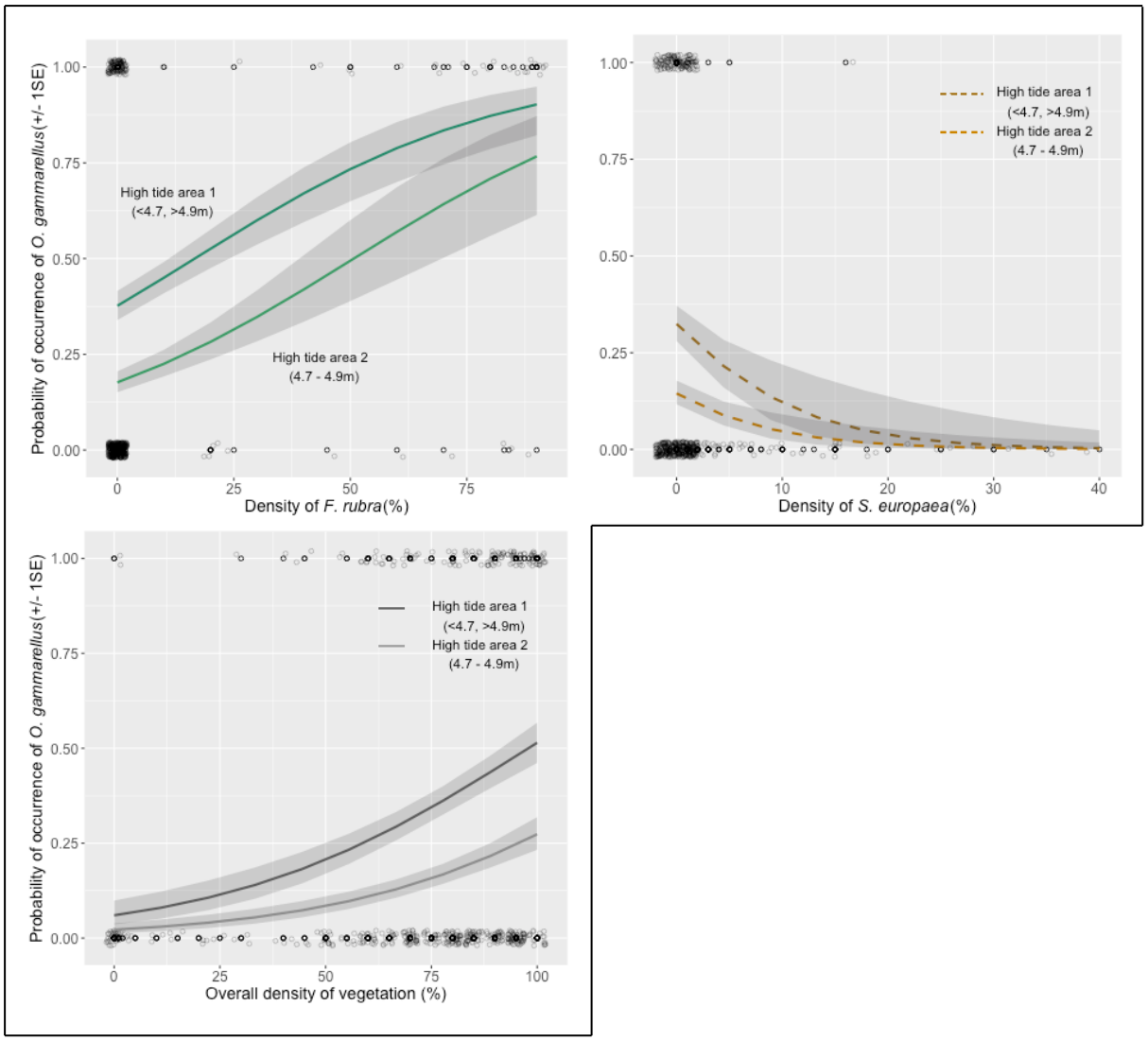


Figure 2.16 *Vegetation and the probability of O. gammarellus occurrence, for high tide areas 1 and 2. When Y = 1 O. gammarellus is present; when y = 0 it is absent. F. rubra and S. europaea have a positive and negative relationship respectively, but the latter was marginally non-significant, where p = 0.079. Therefore, O. gammarellus probability of occurrence increases for F. rubra, but decreases for S. europaea. The bottom plot shows a positive relationship for overall vegetation density, where the probability of occurrence increases along with vegetation density. The darker the point, the more measurements at that reading, although jittering was used to disperse these points. Parameter estimates and SEs plotted from the model in Table 2.10.*

For *O. mediterranea* the best binomial GLM indicated that the probability of occurrence in *A. maritima* decreased by a factor of 8 between zero and 85% *A. maritima* density, for both high tide areas 3 and 4. This is a species of the mid to outer saltmarsh. In contrast, in both high tide areas, the probability of occurrence of *O. gammarellus* in two mid-marsh species, *S. maritima* and *A. tripolium*, each increased by a factor of 2.2 between species densities of zero and 35% (max) and 20% (max) respectively. Nevertheless, these two species showed only a marginally significant effect of $P = 0.027$ and $P = 0.03$ respectively. The probability of occurrence of *O. mediterranea* in the sample plot, in relation to overall vegetation coverage, increased from 0.16 to 0.42 (high tide area 3) and 0.35 to 0.67 (high tide area 4), between zero and 100% vegetation density (Table 2.11, Figure 2.17).

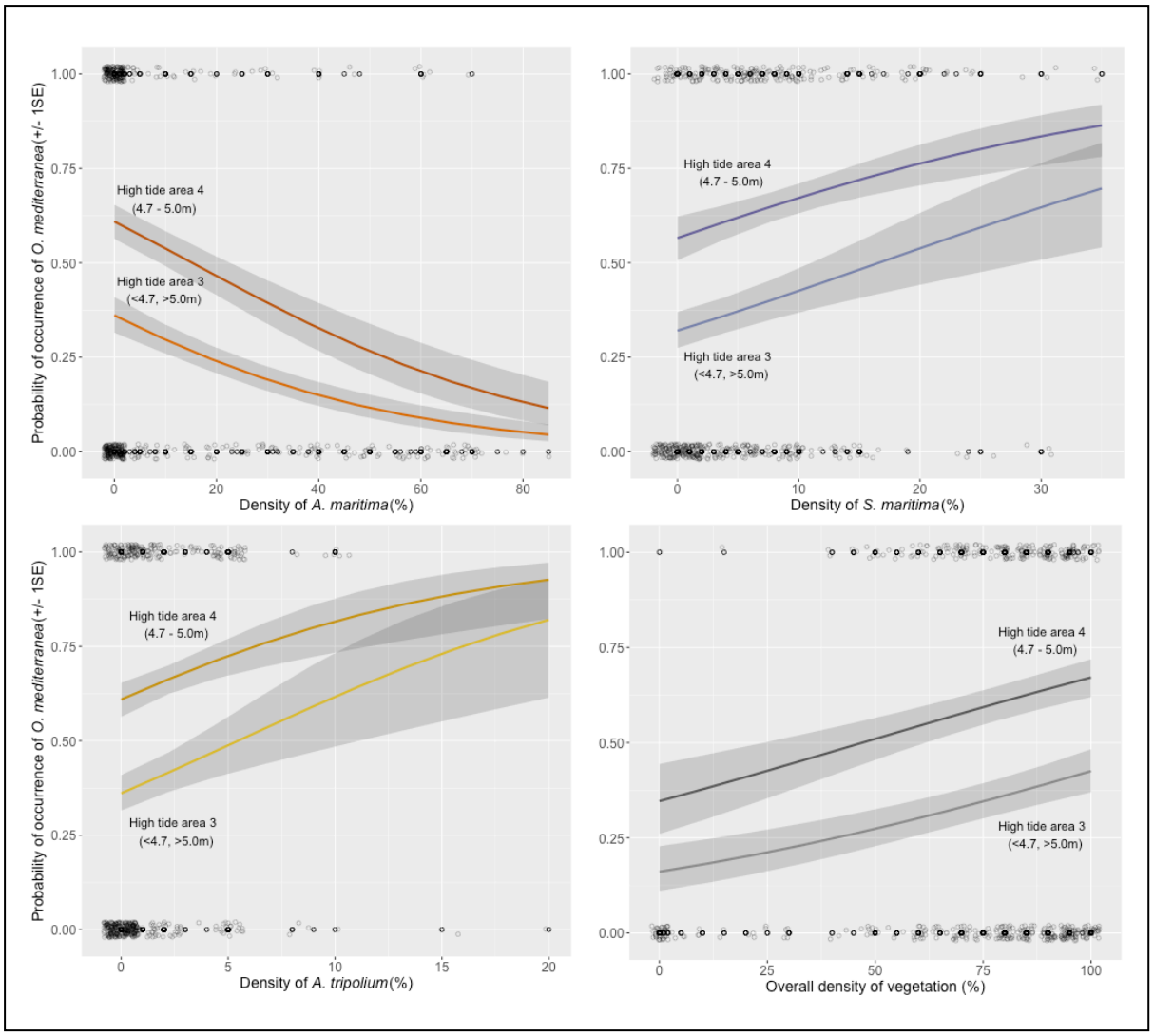


Figure 2.17 *Vegetation density and the probability of O. mediterranea occurrence, for high tide areas 3 and 4. There is a negative relationship for A. maritima where the probability of O. gammarellus occurrence decreases with an increase in vegetation density (top left). In contrast, there is a positive relationship for both S. maritima (top right) and A. tripolium (bottom left), where the probability of occurrence increases with vegetation density. Overall vegetation density (bottom right) also shows a positive relationship. The darker the point, the more measurements at that reading. Jittering was also used to disperse these points. Parameter estimates and SEs plotted from the model in Table 2.11.*

Orchestia abundance and vegetation

O. gammarellus numbers showed a positive quadratic relationship with *F. rubra* which equated to an abundance of 7.7 individuals when *F. rubra* was not present, up to a maximum of 10 individuals at 29% *F. rubra* coverage, before reducing to 2.5 individuals at 90% coverage (Table 2.12, Figure 2.18). *O. gammarellus* abundance compared to *A. maritima*, *P. maritima*, *S. maritima*, *Pl. maritima* and *A. tripolium*, produced a significant negative relationship where numbers of *O. gammarellus* decreased as densities of each species of vegetation increased (Table 2.12, Figure 2.18)

This was contradicted by the results of overall vegetation density in the sample plot, where *O. gammarellus* abundance increased from 2.6 individuals when no vegetation was present to 8.7 individuals at 100% vegetation coverage (Table 2.12, Figure 2.18). The height of vegetation was dropped from the best model.

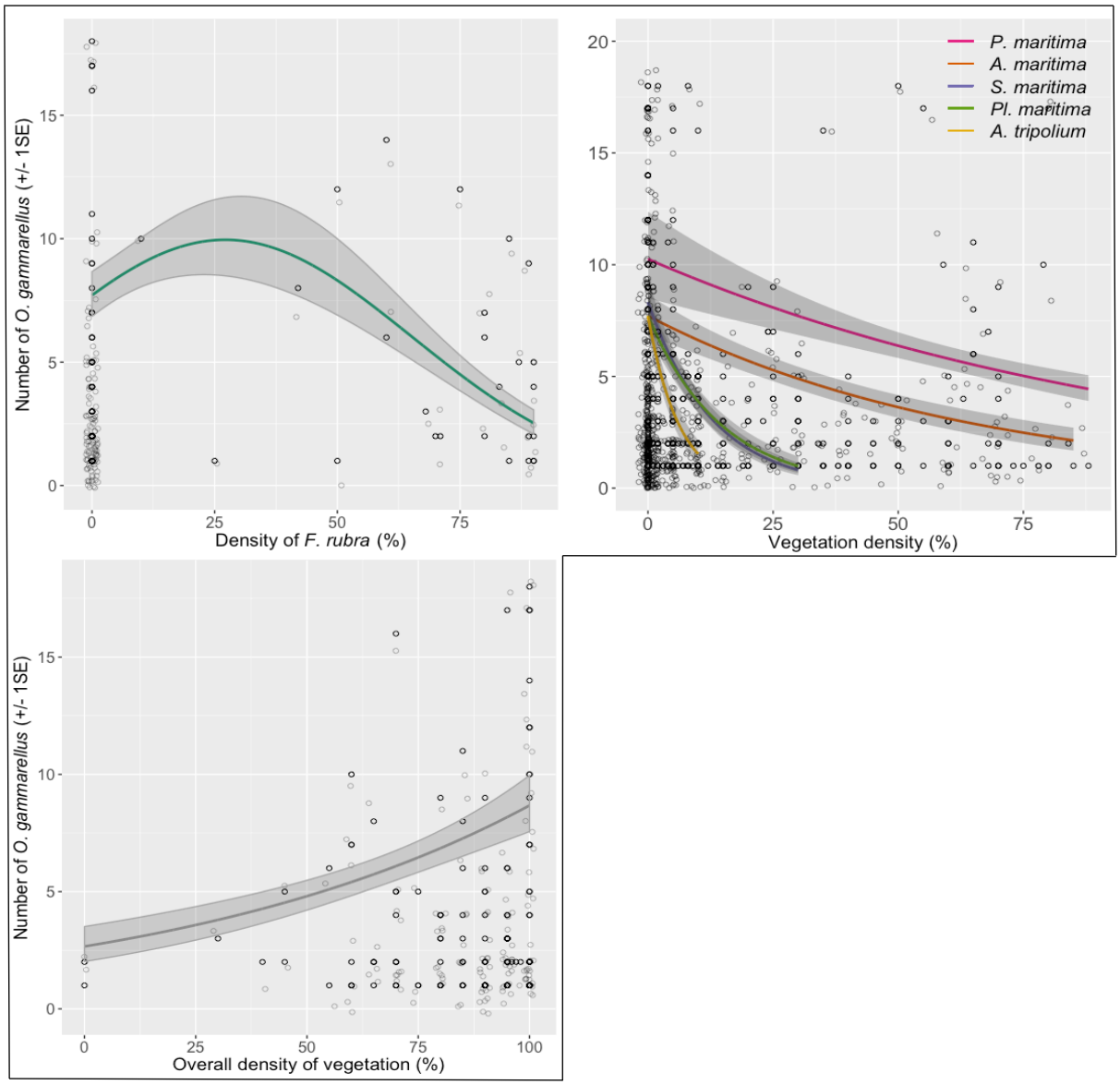


Figure 2.18 *The best poisson GLM for species of vegetation and overall vegetation density and the relationship to O. gammarellus abundance, plotted from the best model (Table 2.12). O. gammarellus abundance shows a significant positive quadratic relationship with F. rubra, and this peaks at about 30% coverage before declining at higher F. rubra densities. Five other species of vegetation all show a significant negative relationship, where abundance of O. gammarellus decreases with an increase in vegetation density for each species. The darker the point, the more measurements at that reading. Jittering was used to disperse some of these points.*

There was a similar pattern in the relationship between *O. mediterranea* abundance and the density of individual species of vegetation to that of *O. gammarellus.* Four species of vegetation showed a significant effect, where an increase in vegetation density saw a reduction in the abundance of *O. mediterranea*. This time *F. rubra* resulted in a decrease in abundance of *O. mediterranea* of just less than 5 individuals when it was not present to 2 individuals at 90% coverage. *A. maritima* indicated 5 individuals when the species was not present to 0.2 individuals at 70% maximum coverage, *P. maritima*, 6.3 individuals when it was not present down to 3.7 at 85% maximum coverage, and *S. europaea* just less than 5 individuals when it was not present down to 0.8 individuals at 40% maximum coverage (Table 2.13, Figure 2.19). In addition, overall vegetation density and vegetation height were dropped from this model.

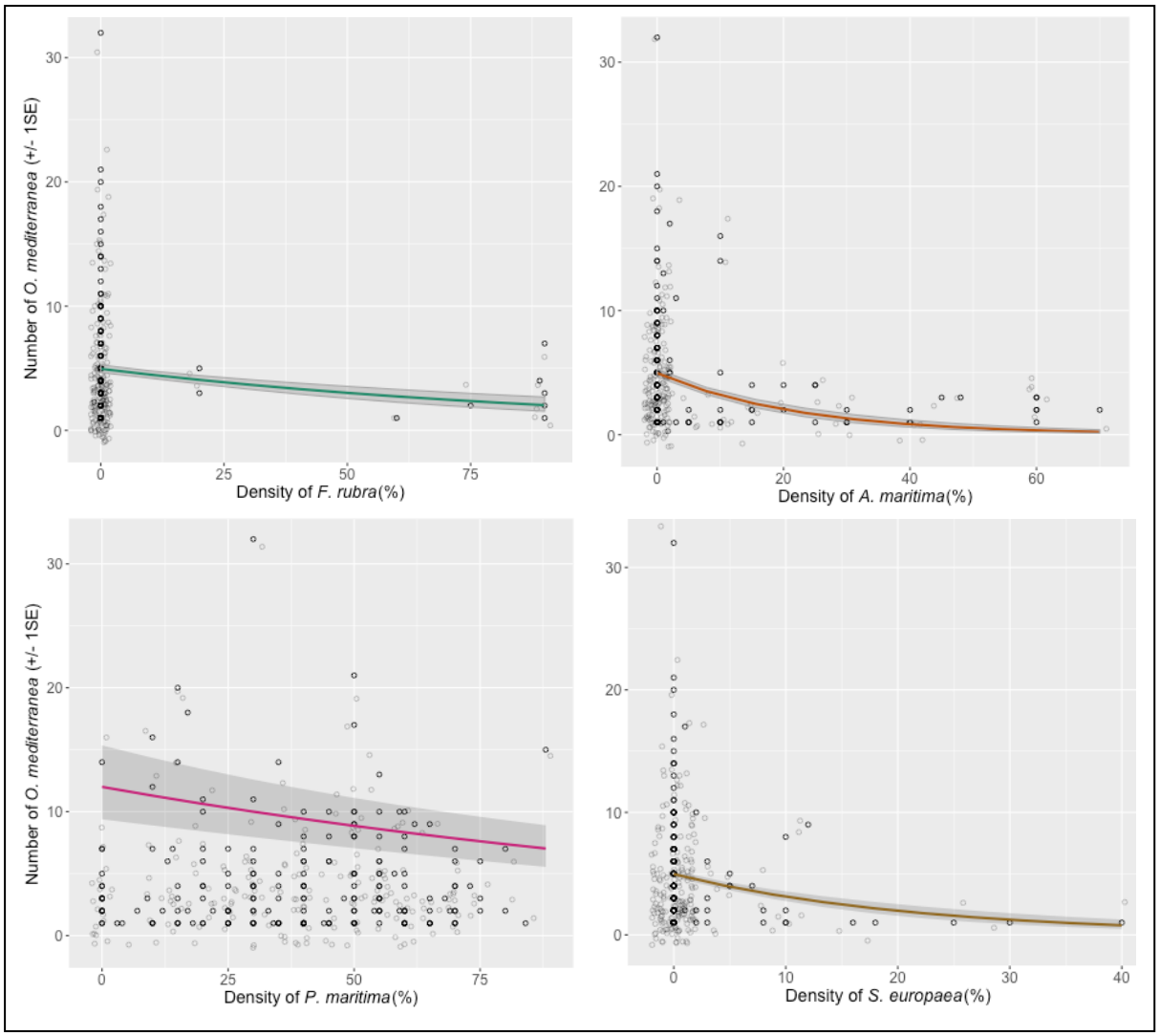


Figure 2.19 *Species of vegetation and their relationship to O. mediterranea abundance. Four species that showed a significant effect in the best poisson GLM, resulted in a negative relationship with increased vegetation density. Parameter estimates and SEs plotted from the model in Table 2.13. The darker the point, the more measurements at that reading. Jittering was used to disperse some of these points.*

Comparison between winters – objective 10

Counts from one hundred winter 1 plots were tested for correlation when the same sample plots were visited in winter 2. Poisson models for each *Orchestia* species showed a significant effect between both years (*O. gammarellus* - est = 0.33, SE = 0.02, $P < 0.01$; *O. mediterranea* - est = 0.26, SE = 0.02, $P < 0.01$ (Figure 2.20).

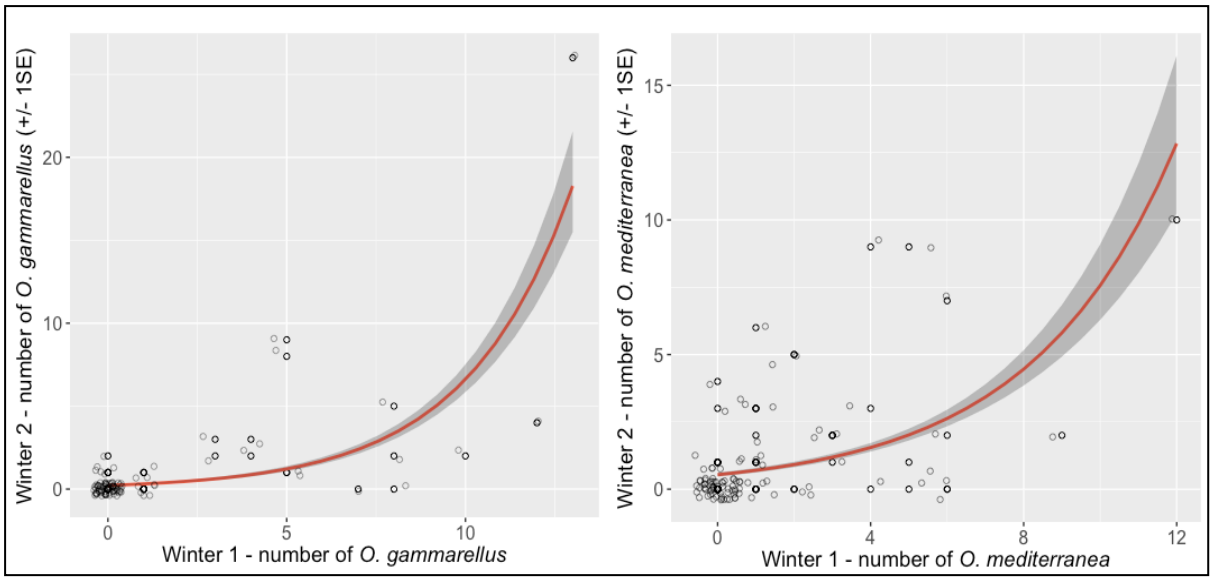


Figure 2.20 *Comparison of 100 counts of Orchestia from winter 1, revisited in winter 2. O. gammarellus (left), O. mediterranea (right). The darker the point, the more measurements at that reading. Jittering was used to disperse points*

2.3.3 Behaviour – objectives 11-13

Orchestia movement and dispersal by tide – objective 11

The data concerning this objective are detailed in Table 2.14.

Table 2.14 *Data from Orchestia movement and dispersal by tide experiment. 42 sample plots were tested – control non-tidal = 9, control tidal = 12, exposed non-tidal = 9, exposed tidal = 12.*

Experiment type	Marked *N*	Mean	SE	Recapture *N*	Mean	SE
Control non-tidal	133	14.78	1.91	72	8.00	1.64
Control tidal	185	15.42	1.75	68	5.67	1.10
Exposed non-tidal	115	12.78	1.50	47	5.22	1.15
Exposed tidal	163	13.58	1.75	17	1.42	0.67

The mark-recapture model indicated that the only sample plots that showed significant effects were *control non-tidal* (*i.e.* covered plots not exposed to the tide) and *exposed tidal* (*i.e.* open plots covered by the tide). The proportion of marked *Orchestia* recaptured under *control non-tidal* was 0.53 compared to 0.14 for *exposed tidal* conditions. Tukey post-hoc tests also showed that recapture rates were significantly reduced between *control tidal, control non-tidal* and *exposed non-tidal* when compared to *exposed tidal*, at the $p < 0.05$ level (Table 2.15, Figure 2.21).

Table 2.15 *The best linear model from the mark-recapture experiment to assess Orchestia movement and dispersal by tides, using control (covered) plots and open plots.*

Variable	Estimate (Log)	SE(Log)	*t*	*P*
Intercept	-0.64	0.18	-1.3	**0.001**
Control tidal	-0.28	0.24	-1.6	0.253
Exposed non-tidal	-0.21	0.26	-0.8	0.434
Exposed tidal	-1.33	0.24	-5.4	**<0.001**

Significant *P* values are marked in bold. Intercept includes categorical level, "Control non-tidal". The Adjusted R^2 for this model is 0.58. Degrees of freedom 38. Model offset was used as the log of those originally marked.

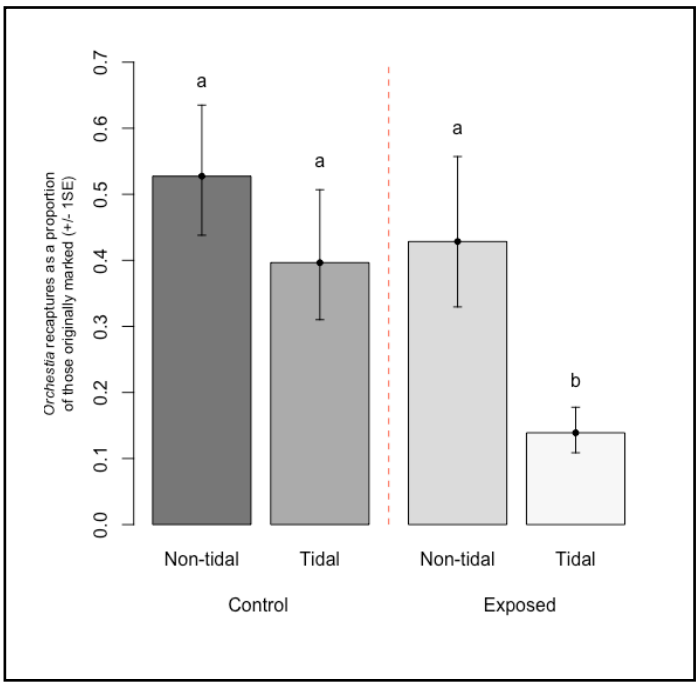


Figure 2.21 *Mark-recapture of Orchestia assessing movement, and dispersal by tide. Some control (covered) plots were not covered by tides and some were, and the same for exposed plots. Control non-tidal, control tidal and exposed non-tidal showed no significant effects. Parameter estimates and SEs plotted from the model in Table 2.15. Tukey post-hoc tests carried out and the same letters indicate no statistically significant difference between those variables. The results showed that exposed tidal was significantly different from the other three treatments.*

Orchestia depression after redshank foraging – objective 12

The data for this experiment are shown in Table 2.16.

Table 2.16 *Data for the Orchestia depression experiment where counts of Orchestia were taken immediately after redshank feeding and then upon a second visit to the same plot*

Number of plots = 26	1st visit			2nd visit		
	Number of *Orchestia*	Mean	SE	Number	Mean	SE
All *Orchestia*	210	4.04	0.70	149	2.87	0.64
O. gammarellus	130	5.00	1.13	83	3.19	0.98
O. mediterranea	80	3.08	0.80	66	2.54	0.83

The best quasi-poisson GLMs showed that there was no significant long-term effect on the numbers of *Orchestia* found in redshank feeding sample plots following revisits to the same plot. The time between first and second visits (24 to 48 hours later) was dropped from the full model because it had no significant effect. This was true when both *Orchestia* species were modelled together, and separately (Table 2.17).

Table 2.17 *Best quasi-poisson model for disturbance to sample plots by redshank feeding. Orchestia were modelled together and separately.*

Species	Variable	Estimate (Log)	SE (Log)	*t*	*P*
Both together	Intercept	2.10	0.15	13.7	**<0.001**
	Second visit	-0.35	0.24	-1.5	0.145
O. gammarellus	Intercept	1.61	0.23	6.8	**<0.001**
	Second visit	-0.45	0.38	-1.2	0.240
O. mediterranea	Intercept	1.12	0.28	4.0	**<0.001**
	Second visit	-0.19	0.41	-0.5	0.643

Significant *P* values are marked in bold. Intercept = first visit. The pseudo R^2 for the models are 0.04 (both species together), 0.03 (*O. gammarellus*) and 0.01 (*O. mediterranea*). Degrees of freedom 50 (both models).

Weather and its effect on Orchestia behaviour – objective 13

Inactivity and jumping behaviour

The raw data for determining *Orchestia* inactivity and jumping behaviour are shown in Table 2.18.

Table 2.18 *Data results for Orchestia inactive and jumping behaviour experiment*

Number of plots = 120	Number of *Orchestia*	Mean	SE
Surface inactive	414	3.45	0.46
Surface jumping	122	1.02	0.20
Subsurface inactive	142	1.18	0.19
Subsurface jumping	41	0.34	0.08
Total	719		

The best poisson GLM predicting the number of inactive *Orchestia* on the surface, showed that this number decreased nearly 14-fold from 3.6 to 0.3 individuals as air temperature increased (2.2°C min to 15.5°C max), whereas surface jumping *Orchestia* increased from 0.3 to 2.5 individuals over the same air temperature range, where best model was a quasi-poisson GLM. Surface inactive *Orchestia* were also slightly affected by wind speed, where they increased in number by from 1 to 1.5 individuals, between 0 mph (min) to 24.1 mph (max). The interaction between air temperature and wind speed also showed a significant effect, where at maximum wind speed, the number of inactive *Orchestia* was 1.1 increasing to 2.2 between 2.2°C (min) and 15.5°C (max). However, at minimum wind speed, the number of inactive *Orchestia* decreased substantially from 5.9 to 0.1 individuals between the same air temperatures (Table 2.19, Figure 2.22).

Table 2.19 *Surface inactive Orchestia and their behaviour when affected by air temperature and wind speed (poisson GLM), and surface jumping Orchestia affected by air temperature (quasi-poisson GLM).*

Surface Inactive				
Variable	Estimate (Log)	SE(Log)	*z*	*P*
Intercept	2.42	0.33	7.3	**<0.001**
Air temperature	-0.29	0.05	-5.9	**<0.001**
Wind speed	-0.10	0.04	-2.4	**0.016**
Air temperature*wind speed	0.01	0.01	2.6	**0.009**
Surface Jumping				
Intercept	-1.39	0.61	-2.3	**0.023**
Air temperature	0.15	0.06	2.6	**0.010**

All *P* values are significant. **Surface inactive model**: Pseudo-R^2 (explained deviance) = 0.16; degrees of freedom 116; AIC: 474 full model, AIC: 468 best model; variables removed from full model – soil temperature, soil temperature* wind speed, air temperature*wind speed, day number. **Surface jumping model**: Pseudo-R^2 (explained deviance) = 0.08; degrees of freedom 118; AICs for quasi-poisson models not provided preventing model selection based on this criterion; variables removed from full model – soil temperature, wind speed, day number, soil temperature*wind speed, air temperature*wind speed, air temperature*soil temperature.

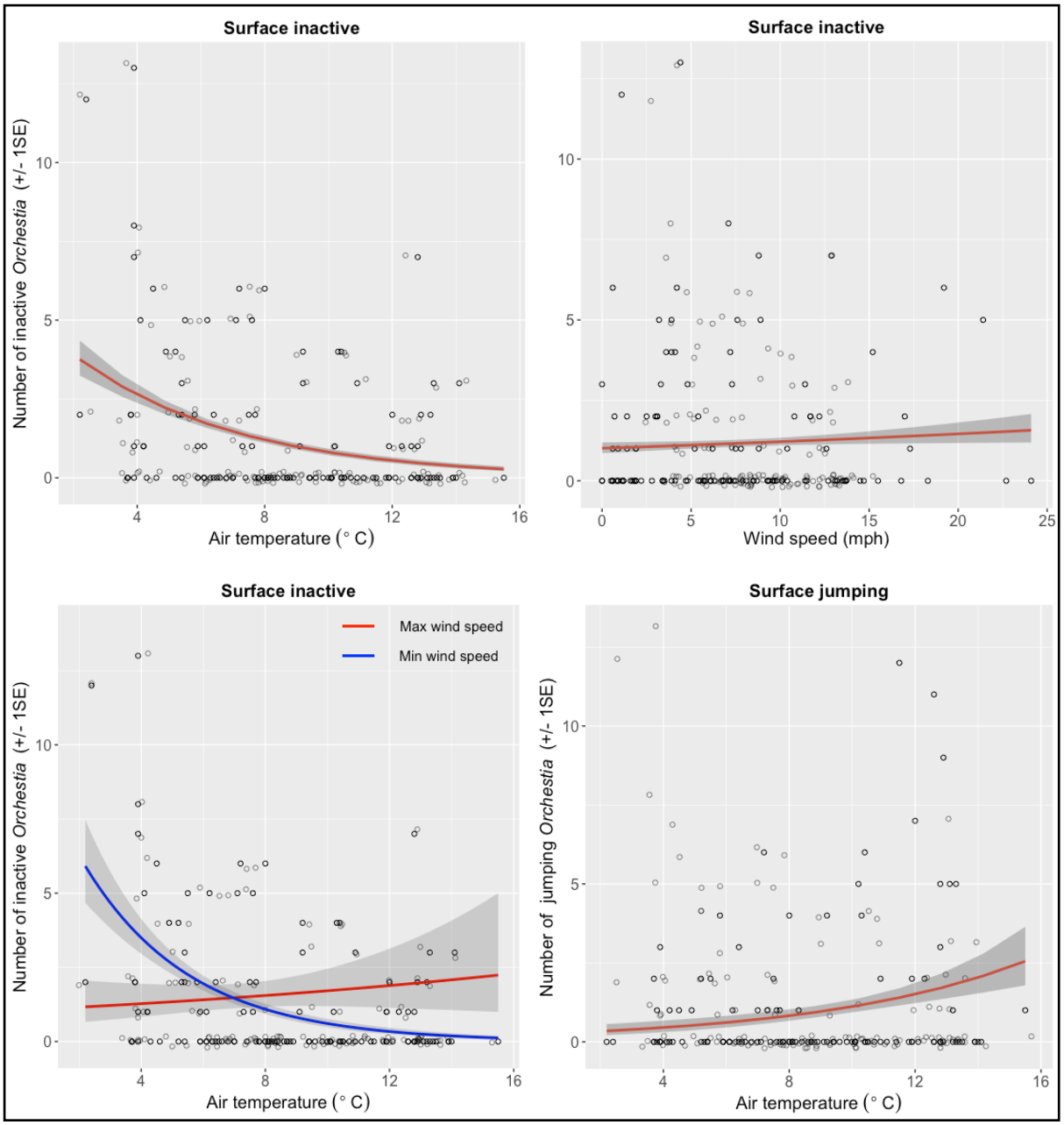


Figure 2.22 ***Surface inactive Orchestia****. Top left and right: Air temperature and wind speed, and bottom left: the interaction between air temperature and wind speed, and their effect on surface inactive Orchestia****. Surface jumping Orchestia****. Bottom right: Air temperature and its effect on surface jumping Orchestia. The darker the point, the more measurements at that reading. Jittering was used to disperse these points. Parameter estimates and SEs plotted from the model in Table 2.19.*

The best models for subsurface inactive and jumping *Orchestia*, were both poisson models. Subsurface inactive results indicated that inactivity decreased as soil temperature increased, from 2.2 active individuals down to 0.2 between 1.6°C (min) and 16.2°C (max). The number of subsurface jumping *Orchestia* increased along with soil temperature from almost zero to 1.4 individuals between the same temperature range. The effect of wind speed on jumping *Orchestia* was marginally non-significant at $P = 0.053$ (Table 2.20 and Figure 2.23).

Table 2.20 *Subsurface inactive Orchestia and their behaviour when affected by soil temperature (poisson GLM), and subsurface jumping Orchestia affected by soil temperature and wind speed (poisson GLM)*

Subsurface Inactive				
Variable	Estimate (Log)	SE(Log)	*z*	*P*
Intercept	0.55	0.23	2.4	0.016
Soil temperature	-0.13	0.03	-4.6	<0.001
Subsurface Jumping				
Intercept	-2.81	0.66	-4.2	**<0.001**
Soil temperature	0.22	0.06	3.9	**<0.001**
Wind speed	-0.06	0.03	-1.9	0.053

P values in bold are significant. **Subsurface inactive model**: Pseudo-R^2 (explained deviance) = 0.10; degrees of freedom 118; AIC: 276 full model, AIC: 276 best model; (likelihood ratio test: χ^2=12.2, *P*=0.06); variables dropped from full model – air temperature, wind speed, air temperature*wind speed, soil temperature*wind speed, air temperature*soil temperature, day number. **Subsurface jumping model**: Pseudo-R^2 (explained deviance) = 0.13; degrees of freedom 117; AIC: 195 full model, AIC: 194 best model; (likelihood ratio test: χ^2=8.88, *P*=0.11); variables dropped from full model – air temperature, air temperature*wind speed, soil temperature*wind speed, air temperature*soil temperature, day number.

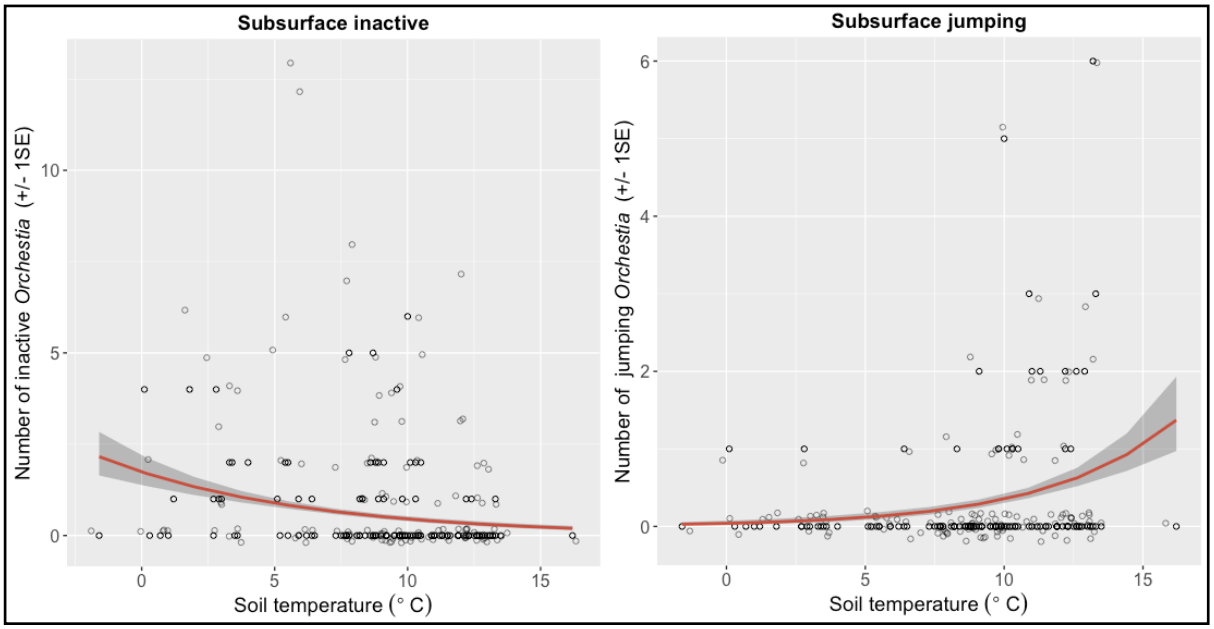


Figure 2.23 ***Subsurface Orchestia****. Soil and its effect on inactive Orchestia (left) and jumping Orchestia (right). Parameter estimates and SEs plotted from the model in Table 2.20. The darker the point, the more measurements at that reading. Jittering was also used to disperse these points for clarity.*

Speed of movement

The data for this part of the research are shown in Table 2.21.

Table 2.21 *Data results for Orchestia speed of movement of experiment.*

Number of plots = 32	*N Orchestia*	Mean *N Orchestia*/plot	SE
Quick-moving Orchestia	252	0.52	0.09
Slow-moving Orchestia	391	1.06	0.10
Total	643		

The best GLMM models indicated that the number of *Orchestia* that did not move or crawl slowly (slow-moving) decreased over 5-fold from 1.6 to 0.3 individuals between air temperatures of 3.1°C (min) and 14.1°C (max), whereas the number that crawled quickly or jumped (quick-moving) increased over 8-fold from 0.3 to 1.6 individuals within the same air temperature range (Table 2.22, Figure 2.24).

Table 2.22 *GLMM models with a poisson distribution for slow-moving and quick-moving Orchestia.*

Slow-moving				
Variable	Estimate (Log)	SE(Log)	*z*	*P*
Intercept	0.96	0.18	5.2	**0.001**
Air temperature	-0.15	0.03	-5.5	**0.001**
Quick-moving				
Intercept	-2.23	0.39	-5.6	**0.001**
Air temperature	0.19	0.05	3.8	**0.001**

All *P* values are significant. **Slow-moving**: R^2 variance explained by random factors = 0.06, R^2 variance explained by fixed effects = 0.20, total = 0.26; degrees of freedom 385; AIC: 934 full model, AIC: 928 best model; variables dropped from full model –soil temperature, wind speed, air temperature*wind speed, soil temperature*wind speed, air temperature*soil temperature, day number. **Quick-moving**: R^2 variance explained by random factors only = 0.11, R^2 variance explained by fixed effects only = 0.13, total = 0.24; degrees of freedom 385; AIC: 844 full model, AIC: 835 best model; variables dropped from full model –soil temperature, wind speed, air temperature*wind speed, soil temperature*wind speed, air temperature*soil temperature, day number.

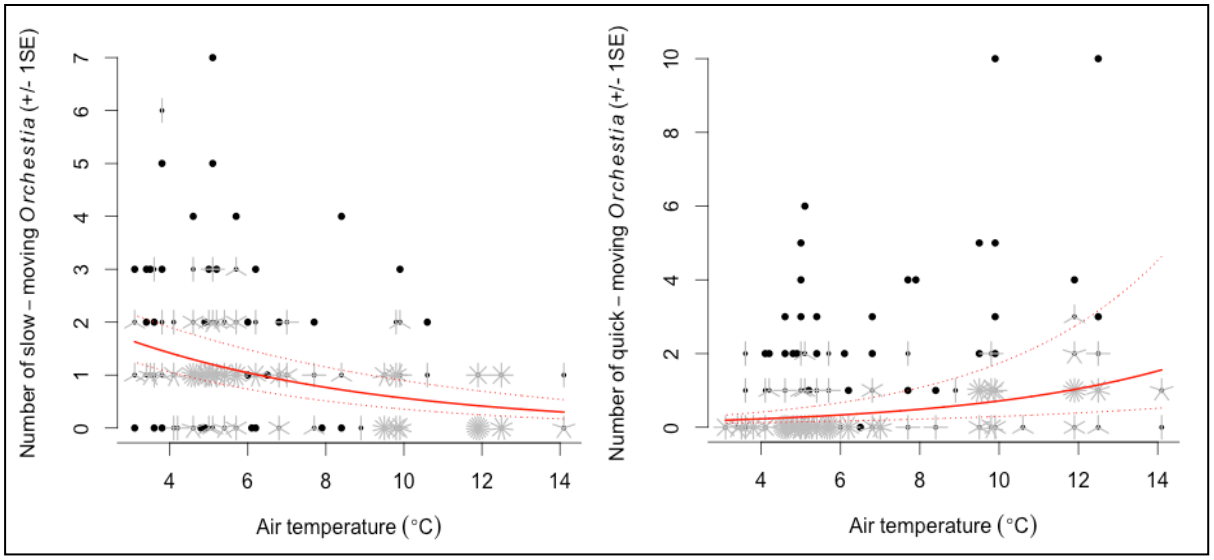


Figure 2.24 *Speed of movement of Orchestia and its relationship to air temperature. Slow-moving (left) and quick-moving (right). Parameter estimates and SEs plotted from the model in Table 2.22.*

2.3.4 Summary of results

Size and composition of Orchestia

The hypothesis in objective 1 is supported where *Orchestia* are sexually dimorphic, with males being larger than females, this being the case for both species. *O. gammarellus* was the larger species when males and females were compared with those of *O. mediterranea*, but this size difference was not apparent in juveniles. In addition, although ratios of male to female and adult to juvenile *O. gammarellus* were not significantly different across the three winters of the research, *O. mediterranea* composition was less predictable and produced significant

differences between winters (objective 2). The hypothesis in objective 3 stated that larger adult *Orchestia* should be found in redshank feeding areas because redshanks purposefully select these feeding patches. The results showed no significant effect for *O. gammarellus* so the hypothesis was not proven for this species, whereas for *O. mediterranea*, the results were contradictory with larger individuals being found in redshank feeding areas in winter 2, but individuals were smaller in these areas in winter 3. Moreover, redshanks do not select larger *Orchestia* when foraging because there was no size difference between samples taken immediately after foraging and second visits, which disproves the hypothesis in objective 4.

Distribution of Orchestia

The expected difference in distribution between the *Orchestia* species (objective 5) was upheld where *O. gammarellus* was most likely to occur in the outer marsh, but surprisingly also in the inner marsh, a finding which was not expected. The hypothesis for *O. mediterranea* was proven in that it was more likely to occur and was more abundant, in the mid marsh. Although *O. gammarellus* was more likely to occur closer to the creek edge, this is in conjunction with medium to high densities of vegetation; at lower vegetation densities, the species was less likely to be present, although only slightly. For *O. mediterranea* the result was clearer where the probability of occurrence decreases with distance, which was more so in its preferred mid-marsh area compared to the inner and outer marsh. For both species abundance increased closer to the creek edge. Therefore, the hypothesis in objective 6 was proven. The hypothesis in objective 7 that occurrence and abundance will decrease in mid-winter was dependent upon the species. *O. gammarellus* was less likely to be found as winter progressed, whereas *O. mediterranea* abundance decreased slightly in autumn before increasing in January.

Each *Orchestia* species tended to occur in different types of vegetation. This partly proved the hypothesis in objective 8 that *Orchestia* prefer species that resemble their own tolerances to seawater, but contradictorily, *O. gammarellus* was more likely to be present in both the outer marsh which receives fewer tides and the inner marsh which receives the most. In contrast, *O. mediterranea* was more likely to occur in vegetation that is associated with the mid-marsh region. Regarding abundance, both species of *Orchestia* were generally fewer in number as coverage of one species of vegetation within their own habitats became dominant, except for *F. rubra* where *O. gammarellus* abundance increased in *F. rubra* from zero to about 30% coverage before decreasing again above this density. Therefore, although the likelihood of *Orchestia* occurrence in specific species of vegetation was proven, an increase in abundance in this vegetation was not. Objective 9 hypothesised that *Orchestia* prefer denser and higher vegetation. Although, the probability of *Orchestia* being present increased in denser vegetation, only the abundance of *O. gammarellus* increased with vegetation density. This variable was dropped in the best *O. mediterranea* model for abundance. Therefore, the hypothesis was partly proven. Furthermore, for both species of *Orchestia*, the height of vegetation showed no significant effect in any of the best models disproving the hypothesis that *Orchestia* may prefer higher vegetation which impedes the activity of predators. When the distribution and density of *Orchestia* was tested to determine if this changed between winters, there was no significant difference between winters 1 and 2, which proved the hypothesis in objective 10.

Orchestia behaviour

Although *Orchestia* may move outside their immediate area by their own locomotion, it was tidal coverage that had the greatest effect of dispersing *Orchestia*, proving the hypothesis in objective 11. The objective 12 hypothesis that prey resource depression occurs as foraging redshanks move across an area was not proven because there was no significant effect for either *Orchestia* species. The hypothesis of objective 13 that *Orchestia* jump more in warmer temperatures and when wind speed is reduced was proven where the number of *Orchestia* jumping increased when the air temperature was higher. It was also proven that wind had an effect where *Orchestia* became less active on the soil surface with an increase in wind speed. Soil temperature was the controlling factor for *Orchestia* activity in the soil where they jumped more when disturbed at higher the soil temperatures. Finally, *Orchestia* moved quicker when air temperature increased.

2.4 Discussion

2.4.1 Size and composition considerations of *Orchestia* populations

Over 3 winters at the study site, the mean size of adult *Orchestia* males was larger than the mean size of adult females (Table 2.5, Figure 2.6). Previous research only gives maximum sizes. Hence, males were larger than females on the Medway estuary, for both species, (Wildish, 1969) and similarly on the Ria Formosa saltmarsh in southern Portugal for *O. gammarellus* (Dias and Sprung, 2004). Table 2.23 illustrates maximum size measurements from these two studies along with those from the study site. Measurement of *Orchestia* in the previous research was conducted using the same methods as this research (see 2.2.3)

Table 2.23 *Maximum size of Orchestia found in this and previous research*

Research	Medway (Wildish, 1969)		Ria Formosa (Dias and Sprung, 2004)		Tyninghame (this study, 2013 – 2017)	
Size (mm)	Male	Female	Male	Female	Male	Female
O. gammarellus	22	18	17	14	19	17.5
O. mediterranea	21	19.5	-	-	18	18

Maximum size at the study site showed that the largest *O. gammarellus* male was larger than the largest female, but for *O. mediterranea* both were 18mm. Therefore, the mean size of *Orchestia* taken over an extended period is probably a more accurate measure of size of those populations. Moreover, for amphipods, latitude has been seen to positively correlate with size (Bergmann, 1847; Poulin and Hamilton, 1995), so it would be expected that *Orchestia* at the study site should be larger than the same species further south. Although this is the case for Ria Formosa (Dias and Sprung, 2004), on the Medway in southern England, *O. gammarellus* and *O. mediterranea* were larger (Wildish, 1969).

This sexual dimorphism seen in amphipods, where the male is larger, usually indicates amplexus in the species (precopulatory guarding of the female by the male). This occurs for several days before the female moults and the male fertilises her eggs, and the greater size enables the male to better subdue the female (Hurley, 1968; Conlan, 1991; Dinning *et al.*, 2003; Cothran *et al.*, 2013). Furthermore, because larger female *O. gammarellus* can produce more eggs and larger broods (Persson, 1999), a trait found in many amphipods (Steele and Steele, 1991), larger males are more likely to mate with larger females. The evolutionary process then results in larger recruits to the population in future generations (Dinning *et al.*, 2003). Despite this, larger male arthropods could be more conspicuous to predators, as has been suggested for arthropod *Gammarus minus* (Glazier, 1999).

The results suggest that redshanks were not selecting *Orchestia* based on size (pages 43-45). Despite this, redshanks select larger *Corophium* (Goss-custard, 1967) and *Nereis* worms (Goss-Custard, 1977a), so one would expect them to select larger *Orchestia*, and concentrate feeding effort in habitat that contained the larger species (*O. gammarellus*), and larger males. Yasue *et al*. (2003) suggested that redshanks preferred to forage adjacent to creek edges inhabited by dense grass (*F. rubra*) because these areas held larger *Orchestia* (11-15mm). The

estimated number of *Orchestia* in the study area, found by averaging the number in the 10cm x 10cm quadrats in winter 1 (points 301 to 700 only, estuary excluded), is approximately 640,220 (2.38 per $10cm^2$ x field study area - $2690m^2$). It is possible that such a large *Orchestia* population is impacted by redshank depredation, but more importantly, it may temporarily reduce larger individuals in some feeding patches that are foraged regularly, which will not be redistributed from other areas until the next tidal coverage (2.3.3, pages 59-60). Predation of large *Orchestia* may also be compounded by the effect of other species, especially curlew which forage on the saltmarsh and are ever-present, numbering around 12. However, the size of *Orchestia* in feeding plot samples taken immediately after redshanks had left after feeding was no different to that upon the revisit. This offers no evidence that redshanks are choosing larger *Orchestia*, or that larger *Orchestia* are reoccupying a patch from the surrounding marsh once foraging redshanks have moved on. Although Minderman *et al*. (2006) discovered that *Orchestia* numbers were depressed temporarily for just a few hours, redshank feeding rate soon returned to the previous levels, but no evidence was presented that larger *Orchestia* were better able to escape, or were being specifically targeted. The results also showed that the size of *O. gammarellus* in redshank feeding areas was no different to non-feeding areas, and that *O. mediterranea* were larger in feeding areas in winter 2, but smaller in winter 3 (Table 2.7, Figure 2.9). This would suggest that redshanks were not selecting *Orchestia* based on size. Nevertheless, Goss-Custard (1977b) found that redshanks spent between 88 and 96% of daylight hours feeding in winter almost exclusively on *Corophium*, taking between 50 and 70 per minute. This equates to between 40,000 to 60,000 in a 24hr period (Goss-Custard, 1977c). It is unlikely that redshanks searching and probing for *Orchestia* take the same number of prey items, but this does suggest some negative density dependent control, possibly of large *Orchestia*. A further consideration is that over the 3 winters, females outnumber males by 1.6:1 for *O. gammarellus* and 1.4:1 for *O. mediterranea* (Table 2.4), so this might add weight to the argument that the larger males are being preferentially targeted by redshanks, although perhaps it is more likely that sex determination and in this case female bias, is regulated by selective male mortality and not attributed to predation, and/or complex sexual genetics (Ginsburger-Vogel and Charniaux-Cotton, 1982; Moore and Francis, 1986b).

2.4.2 Influences on the distribution of *Orchestia*

Orchestia zonation in relation to high tide height and elevation

The preferred positions of *O. gammarellus* on the outer and *O. mediterranea* on the mid and inner saltmarsh agrees with much of the previous research which indicates that these species occupy two distinct zones – upper shore and lower shore (Figures 2.10, 2.11 and 2.12) (Jones, 1948; Den Hartog, 1963; Wildish, 1969, 1972; Bradley, 1974). Likewise, although distinct, there is some overlap between the zones which has been noted for other saltmarsh animals (Daiber, 1977; Kneib, 1984), and although interspecific competition between invertebrates has been recorded (Willason, 1981; Brenchley and Carlton, 1983; Stiling *et al*., 1991; Denno and Roderick, 1992), it is thought to be relatively unimportant in defining the zonation of species (Vince *et al.*, 1976; Kneib, 1984); more likely this is determined by environmental stresses (*e.g.* tide) and availability of food (Davis and Gray, 1966; Denno, 1977). Tidal coverage should theoretically be linked to the elevation of the shore, in that neap tides cover lower elevations and spring tides extend to the highest elevations. However, elevation was removed from the distribution models as having no significant effect, which presented an anomaly. But this can probably be explained by subtle changes in saltmarsh relief across small areas, although differential GPS elevation

measurements were very accurate (error = +/- 3cm), subsequent use of ArcGIS interpolation methods, smoothed out the digital relief between points leading to a misrepresentation of the ground truth. An example of this is creek edges which are noticeably higher than surrounding marsh, but to accurately map their elevation would require GPS readings to be taken every few centimetres, which is impractical.

Tidal inundation may affect the distribution of *Orchestia* because this offers an opportunity for predation by fish. Gobies (Gobiidae) can be classed as saltmarsh residents and occur throughout the year (Stevenson, 2002), so invertebrates including *Orchestia* probably provide an important food source. Elliott *et al*. (1990) used three terms to describe the usage patterns of the 36 species that inhabit estuarine waters in the Firth of Forth – marine straggler, migrant and marine opportunist. Opportunists are particularly important; fish larvae that drift into estuaries and live on or just off the bottom. These are termed O group fish, less than 12 months old, which use saltmarshes as nursery feeding grounds, before moving out to open water to begin their life as adults (Little, 2000). In the Firth of Forth these species may be Gadoids, and include cod (*Gadus morhua*) and whiting (*Merlangius merlangus*); flatfish such as plaice (*Pleuronectes platessa*) and common dab (*Limanda limanda*); but also adult clupeids, sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) (Elliott *et al*., 1990). It is thought that fish limit the distribution and numbers of invertebrates across the saltmarsh habitat when covered by tide (Bell *et al*., 1978; Bell, 1980; Posey and Hines, 1991). This predation is much greater in the inner saltmarsh and invertebrate distribution is therefore mainly limited to the mid and outer marsh where foraging by predatory fish is reduced and denser vegetation provides protection for prey (Bell, 1980; Kneib, 1984, 1994; Lin, 1989; West and Williams, 1986). One would expect the greatest impact to be upon *O. mediterranea*, because it is mainly a mid-marsh species, and although high densities occur in some areas of inner marsh, it is absent in others, especially around the mouth of the main creek (Figure 2.10). It is suggested that this relates to vegetation coverage of *P. maritima* grass and where this occurs in the inner marsh it provides a refuge for *Orchestia* during tidal coverage. This grass is very sparse at the mouth of the main creek so offers little protection for *Orchestia* from foraging fish, which might take advantage of *Orchestia* washed out of thicker vegetation by the tidal flow and ebb. However, no evidence can be seen from Figure 2.10 of a low to high gradation of general abundance from inner to outer marsh.

Preference for certain species of vegetation and the creek edges

Orchestia species prefer different types of vegetation (Tables 2.9 and 2.10, Figures 2.16 and 2.17), whose position on the saltmarsh is reflective of the amount of tidal coverage they receive, which is also an indicator of their salt tolerance levels, and specifically their ability to deal with salt concentrations and immersion in saltwater. *O. mediterranea* may be more salt-tolerant than *O. gammarellus,* but Weeks and Rainbow (1992) indicate that both have a high tolerance. *O. gammarellus* is more likely to be present in *F. rubra* as this grass gets denser. It is probable that this species is *F. rubra litoralis*, the most salt-tolerant of three sub-species and the one likely to occur on saltmarshes (Adam, 1993). This contradicts previous research on saltmarshes where *O. gammarellus* has been associated with *P. maritima* (Den Hartog, 1963) and *P. maritima* and *S. maritima* mixed habitat (Moore and Francis, 1985; Creach *et al*., 1997). The reason that *F. rubra* occurs on the outer marsh is that it is less salt-tolerant than other saltmarsh plants (receives fewer tides), and less able to cope with submergence and waterlogging; therefore it grows at higher elevations and on quick-draining soils (Adam, 1993). It is most prevalent to the south west close to Little Binning wood and to the north, where it is associated with two of the

densest areas of *O. gammarellus*, but whereas the south west position is at a higher elevation (6 to 8m), the northern one shows the lowest elevation on the saltmarsh (0 to 0.5m). This might seem inconsistent but the northern saltmarsh holds a multitude of small creeks, and creek edges form levees that are higher than the surrounding marsh. The levees are created because as the creek channel cliff erodes, the sediment is redeposited by high tides, mostly on top of the creek edge (Adam, 1993). *F. rubra* grows well on levees which are well drained and drier, owing to the fact that spring and neap tide water table levels are lower at creek edges (Packham and Willis, 1997). Being drier, creek edges also contain cracks and fissures which are used by *Orchestia* as refuges (pers. obs.). Also, being drier the soil has a higher redox potential (*i.e.* it holds more oxygen) and produces fewer toxic sulphides caused by waterlogging (Chapman, 1960; Howes *et al.*, 1981; Drake, 1989; Adam, 1993; Howes and Goehringer, 1994). This may encourage *Orchestia* to thrive here.

The results regarding the probability of *Orchestia* occurrence and abundance against distance from the nearest creek edge showed an anomaly in that although the abundance of both *Orchestia* species showed a negative correlation with distance, and *O. mediterranea* is more likely to occur closer to the creek edge, *O. gammarellus* does not when entered as a single variable in the model (Table 2.10, Figure 2.13). It does however show a significant effect when entered as an interaction with vegetation density. The probable reason for this is that the *O. gammarellus* area to the south west in *F. rubra* habitat is devoid of creeks, which in the model nullifies the effect of them occurring close to creek edges, whereas the interaction between distance and vegetation density identifies the significance of dense patches of *F. rubra* on creek levees in the north, which is a preferred habitat of *O. gammarellus*. Therefore, this might suggest that dense *F. rubra* on the creek edge is a favoured area for this species. In addition, because *F. rubra* occurs in dense mats, a baffling effect occurs where more tidal sediment settles out on creek levees, and this sward not only offers protection to *Orchestia*, but the deposition of organic sediment makes this area rich in food and nutrients (Callaway *et al*., 1996; Day *et al*., 1999).

O. mediterranea is more likely to be found in *S. maritima* and *A. tripolium*, which are species that occupy the mid and inner saltmarsh, and because these plants are covered by more tides, they have a higher salt tolerance than *F. rubra* (Table 2.11, Figure 2.17) (Adam, 1993; Packham and Willis, 1997). It is possible that *O. mediterranea* is physiologically less capable of retaining sodium ions and requires frequent replenishment from seawater and saline foodstuff, so is prevented from extending its range into the outer saltmarsh and *O. gammarellus* habitat. Instead it out-competes *O. gammarellus* in the mid and lower marsh, levels occupied by *S. maritima* and *A. tripolium* (*i.e. O. mediterranea* has a lower upper eurohayline tolerance level than *O. gammarellus*) (Weeks and Rainbow, 1992). Friend and Richardson (1986) and Moore and Francis (1986) alluded to this when they said that it is the physiological inability of many species of Talitridae to retain essential salt ions that prevents them from migrating into semiterrestrial areas. *O. mediterranea* is less likely to be found in *A. maritima*. This is not surprising because the plant occurs in patches amongst *F. rubra* and is also an outer saltmarsh species. The roots are very compact and dense, so it is difficult for *Orchestia* to penetrate below soil level, but because it is found on the outer saltmarsh, *O. gammarellus* is the more likely species to occur here.

Orchestia of both species showed a decline in abundance for several species of vegetation as those species increased in density (Tables 2.11 and 2.12, Figures 2.18 and 2.19). This could be because *Orchestia* prefer habitats

that contain a mixture of different types of vegetation rather than a homogeneous cover of one species. Nevertheless, one would expect *O. gammarellus* to increase in number when *F. rubra* increased in density as it was very much associated with this plant, but this was not necessarily the case, because at higher densities its abundance declined. This may be because when it was found in sample plots containing lower and medium densities of *F. rubra*, these patches were an attractive habitat for *O. gammarellus*, especially if the plot contained bare soil and mats of *A. maritima*, which due to its impenetrable root system does not appear to provide as much shelter and effective protection from the effects of desiccation and predation. In a mixed sward such as this *O. gammarellus* colonies are found in the dispersed patches of *F. rubra*, which because of its dense foliage and loose root filaments can provide better protection. It is suggested that *O. gammarellus* uses these *F. rubra* patches as a refuge in what would otherwise be an unsuitable habitat where their abundance is higher. There are high populations here so that a sample in one of these patches reflects high *F. rubra* density and high *O. gammarellus* abundance. In contrast, when a sample plot contained an extensive homogeneous carpet of *F. rubra*, *O. gammarellus* were dispersed throughout the sward and abundance was reduced.

Preference for certain types of vegetation structure

Vegetation structure showed that for overall density, both *Orchestia* species were more likely to be present in denser vegetation, whereas only *O. gammarellus* abundance increased with vegetation density (Tables 2.9, 2.10, and 2.11, Figures 2.16, 2.17 and 2.18). Desiccation is recognised as a serious threat to Talitridae (Backlund, 1945; Williamson, 1951; Hurley, 1968; Wildish, 1969, 1970a; Moore and Francis, 1986; Morritt and Spicer, 1998; Dias and Sprung, 2004). Therefore, besides thicker vegetation allowing *Orchestia* to hide from predators, it may enable them to remain in a humid environment that reduces desiccation stress. This was noted by Waterhouse (1955) where a matted level of dead grass at ground level could produce a high relative humidity of 90% and calm air which reduced desiccation for invertebrates. This type of matting, commonly seen in *F. rubra* (as mentioned above), may be particularly beneficial to *O. gammarellus*, which like other supralittoral species is more prone to desiccation (Morritt and Spicer, 1998). The model results also show that neither *O. gammarellus* or *O. mediterranea* was more likely to occur, or was more abundant at different vegetation heights (Tables 2.9, 2.10, 2.11 and 2.12). A plant's density of foliage and accessibility to its root system is probably more important to survival of *Orchestia* than the height of that vegetation, even if taller vegetation is unsuitable habitat for redshanks because it may restrict the foraging ability and further restrict their awareness of an attack from predators.

Seasonal and yearly changes in distribution

In winter 1, the probability of *O. gammarellus* occurring decreased between November 2013 and March 2014. Although in winter *Orchestia* may be quiescent (therefore more cryptic) and remain in the soil making them harder to detect, *O. gammarellus* life history may explain why presence decreases. Studies at Millport, Isle of Cumbrae, Scotland, indicate that their breeding season is from the end of April until September (Morritt and Stevenson, 1993; Moore and Francis, 1986b), in Looe, Cornwall it was from April to August (Jones and Wigham, 1993), whereas on the Ria Formosa saltmarsh, Portugal they bred throughout the year (Dias and Sprung, 2004). At higher latitudes, it therefore appears that breeding ends in September, after which time there may be a natural wastage of the population caused by cold temperatures, storm tides and predation, until recruitment to the population in the following spring. If redshanks feed mostly on *Orchestia* every day between early January until

the beginning of March, there may be considerable depredation, dependent upon: the number of redshank feeding; the number of other bird species feeding on *Orchestia*; and abiotic factors such as wind speed and temperature controlling their availability. Initial observations in winter 1 appeared to suggest that redshanks forage mainly on the outer marsh. Therefore, it is assumed that *O. gammarellus* are the species most likely to be eaten, and are predated disproportionately when compared to *O. mediterranea*.

Besides redshanks, other species can also be seen feeding on *Orchestia*, especially curlew and to a lesser extent, common greenshank and Eurasian starlings (*Sturnus vulgaris*). These could all reduce the population until the initiation of the next breeding cycle. Juvenile redshank size in January at Teesmouth was given as 150g by Mitchell *et al*. (2000) and curlew as 410 – 1360g (Dunning Jr, 1992), therefore, if mean curlew weight is taken as 885g, they are almost six times larger than redshanks. Rippe and Dierschke (1997) indicated that curlews took between 1649 and 1824 items per day when feeding on small ragworm (20mg) a larger prey than *Orchesti*a, enabling them to survive, by reaching 3 times their basal metabolic rate. If curlews exclusively took *Orchestia* at the same rate as ragworm, the *Orchestia* food supply would soon be exhausted[1]. Therefore, curlew must be feeding on other prey as described by Cramp and Simmons (1983), such as *Nereis*, *Arenicola*, *Lanice*, *Carcinus*, *Cranagon*, bivalve molluscs and terrestrial invertebrates. Nevertheless, curlews must make a considerable impact upon the *Orchestia* population and in turn, reduce this resource for redshanks.

In contrast, *O. mediterranea* numbers remained constant until mid-winter when they began to increase (Table 2.12, Figure 2.15). Furthermore, Wildish (1969, 1979) indicates that it is likely that in the Medway estuary *O. mediterranea* has a similar breeding periodicity to *O. gammarellus*, so breeding initiation is unlikely to start earlier in the year further north, especially as a longer photoperiod and higher temperatures are initiators of breeding (Moore and Francis, 1986b). It is possible therefore, that *O. mediterranea* is active in mid to late winter because it is covered by more tides in the mid and inner marsh. Sea temperatures are at their coldest in the Firth of Forth in February when they range average is between 5.2 and 7.4°C (World Sea Temperature, 2017), but these could still provide a buffering effect against colder air temperatures. Moreover, it may also be because *O. mediterranea* are not as heavily depredated by redshanks, there are more of them that have overwintered by the beginning of spring.

2.4.3 How *Orchestia* behaviour influences their distribution

Locomotion and zonation of the species

A mass autumn movement of tens of thousands *Orchestia* was witnessed on the rocky shore to the east of the study site, where they moved landward out of a wrack bank to escape a storm tide (pers. obs.). *O. gammarellus* has also been seen to crawl up the shore retreating from an incoming tide (pers. obs.). It appears that both species attempt to escape incoming tides if they are close to the high tide mark and are not always willing to be passively transported to different areas as described by Karlbrink (1969), Wildish (1969), and Henzler and Ingolfsson (2007). Although a poor swimmer *(*Laffaille *et al*., 2005; Henzler and Ingolfsson, 2007), *O. gammarellus* may

[1] If the ragworm intake of 1649 is taken as number of items taken per day by one curlew and there are 12 on the saltmarsh, for the 71- day period in winter 2, this equals 1,404,948 *Orchestia*. Estimated population of the study area is only 640,220.

have a similar strategy to other talitrids when covered by seawater, where it sinks to the bottom and alternates between crawling and immobility. When crawling it can use features (*e.g*. slope) to orientate back to dry land, or remain cryptic by staying motionless and therefore less obvious to benthic fish predators. Remaining on the bottom may also reduce the effects of strong currents and waves (Ugolini, 1989). *O. mediterranea* being a better swimmer (Weeks and Rainbow, 1992) might employ a different strategy. Despite the results of the dispersal experiment which showed that *Orchestia* can be picked up by the tide and deposited elsewhere (Table 2.15, Figure 2.21), the comparison between winters 1 and 2 showed that *Orchestia* numbers were similar in the same areas (page 60, Figure 2.20). Therefore, they may have some ability to maintain their position in normal tidal flow by their own locomotion, or if transported short distances are able to return to their respective habitats, or recruitment to the population in spring enables the species to maintain the carrying capacity of the respective zone.

Depression by foraging redshanks

Minderman *et al*. (2006) found that *Orchestia* respond to disturbance, by retreating into the soil during redshank foraging. During their research, areas were covered with black plastic sheeting resulting in *Orchestia* moving vertically upwards onto the soil surface, and then retreating into the soil when it was removed, simulating behaviour that allows them to escape predation by redshanks. However, what this showed was that *Orchestia* prefer the more humid environment simulated by the plastic sheeting, similar to conditions they might find in piles of wrack. This retreat into the soil was to escape the effects of desiccation, for example a drying wind. Redshank feeding rate reduced when they fed in an *Orchestia* patch but returned to normal sometime later when it was revisited, indicating that *Orchestia* had reappeared on or near the surface. No evidence of this could be found in the *Orchestia* depression experiment where there was no significant difference in abundance between first and second visits to redshank feeding patches (Table 2.17). One explanation might be that Minderman *et al*. (2006) measured feeding rate and not abundance of *Orchestia*. *Orchestia* may become available through redshank disturbance such as pecking and probing which provokes an escape response. *Orchestia* are then easier to detect and are harvested. As mentioned previously, this escape response is to jump several times, crawl for cover and remain still. Once still *Orchestia* become harder to detect and redshanks move onto the next patch. There is scope for further research to discover the exact influence of depression on *Orchestia* numbers by redshank foraging.

The effects of weather

Wind speed and temperature affect the activity and speed of movement of *Orchestia*. Generally, they jump more and move quicker at higher temperatures on the surface and in the soil when disturbed, whereas at lower temperatures they remain curled up and crawl slowly only if provoked (Tables 2.18, 2.19 and 2.21, Figures 2.22, 2.23 and 2.24). Amphipods aim to avoid wind (Hurley, 1968), a desiccating environment which greatly increases the risk drying out, and this has also been noted for talitrids (Morritt and Spicer, 1998), and *Orchestia* (Amanieu and Salvat, 1963; Sprung and Machado, 2000; Colombini *et al*., 2013). Therefore, it appears that by curling up they can reduce size and exposure of the body surface to increased air currents. In addition, increased activity at higher temperatures has been seen in polychaetes and isopods by Pienkowski (1983), and in *T. saltator*, a similar species to *Orchestia*, where 10°C was given as the seasonal threshold for surface activity (Paulluault, 1954).

Higher temperatures promote activity and are responsible for initiating a response from male *O. gammarellus* which go in search of breeding females (Moore and Francis, 1986b) and a critical air temperature of 10°C was given for the onset of this behaviour (Morritt and Stevenson, 1993). Greater activity on the surface may mean that they are noticed and therefore preyed upon by redshanks. Inactivity and reduced movement of *O. gammarellus* at lower air temperatures has been described by Wildish (1969). The habit of *Orchestia* moving into the subsoil and remain curled up when surface temperatures were close to freezing was observed during this study. This also meant that they were harder to detect and more cryptic. The interaction between air temperature and wind speed showed that surface inactivity increased slightly at higher wind speed and higher air temperature, but inactivity decreased in still conditions and higher temperature (Table 2.19, Figure 2.22). Therefore, it would appear to be the drying effect of wind on *Orchestia* that is the greatest threat to desiccation, and not higher temperatures.

2.4.4 Conclusion

In this chapter, *Orchestia* distribution and behaviour and the factors controlling them were investigated to determine the potential role of *Orchestia* in influencing trophic dynamics in a saltmarsh ecosystem, where redshanks predate *Orchestia* and sparrowhawks predate redshanks. *O. gammarellus* was larger than *O. mediterranea* and preferred the outer saltmarsh whereas *O. mediterranea* preferred the mid and inner marsh. Males tended to be larger than females and female to male ratio was as high as 1.6:1. This may be because *Orchestia* males (especially *O. gammarellus*) are preferentially targeted as prey by redshanks, but more likely due to a shorter male lifespan and/or a female biased sex ratio for the species. The extent and frequency of tidal coverage was an important factor in *Orchestia* zonation, possibly determined by different tolerances to desiccation and/or salt water. Elevation measurements were too coarse to accurately illustrate a topographical image of the saltmarsh that could be used as a useful predictor of distribution. Vegetation density and nearness to creek edges showed a positive correlation with *Orchestia* presence and abundance, and different species of vegetation were an indicator of *Orchestia* zones, although abundance reduced in homogeneous habitats of single plant species. The probability of *O. gammarellus* presence decreased throughout the winter, whereas numbers of *O. mediterranea* increased from mid-winter onwards. This might be because tidal inundation in the mid and lower shore buffers *O. mediterranea* against freezing temperatures, enabling it to be more active and easier to detect. There was no inter-annual variability in the species of *Orchestia*, and general abundance of each species when a selection of sample plots in winter 1 were revisited in winter 2. *Orchestia* are moved by the tide but this has little effect on the zonation of the respective species. Depletion of *Orchesti*a numbers by foraging redshanks moving over a patch could not be proven, so although temporary depression of surface numbers may occur. Temperature and wind were drivers of *Orchestia* movement whereby lower temperatures resulted in them being inactive and slower moving as did higher wind speeds. An increase in wind speed results in *Orchestia* becoming more inactive due to a greater risk of desiccation. It is likely that when temperature rises, increased activity may make them more available and detectable to feeding redshanks.

The next chapter will look in detail at feeding redshanks and the variables that predict their distribution, to determine how the same basal abiotic and vegetation predictors that affect *Orchestia* also affect redshanks. This will provide a starting point to understand the dynamics between redshanks and *Orchestia,* and how and why

redshanks expose themselves to the risk of predation from sparrowhawks when feeding on the saltmarsh, as they seek to maintain their energy budgets through foraging in the most profitable areas, particularly as energetic demands increase in cold weather.

CHAPTER 3. PREDICTING REDSHANK DISTRIBUTION ON THE SALTMARSH

3.1 Introduction

Flexible behaviour which enables animals to balance the requirements of energetic intake with the risk of being killed by predators will be favoured by natural selection. Such behavioural flexibility is termed the starvation-predation risk trade-off, and will require an animal to make decisions on where to feed, when best to feed, what to feed on and how to feed (Lima and Dill, 1990; Lima, 1998a). For example, Cowlishaw (1997) described this trade-off in a study that looked at baboons (*Papio cynocephalus ursinus*) in a desert environment that were predated by leopards (*Panthera pardus*) and lions (*P. leo*). Factors of habitat availability, foraging profitability in the daytime and at night, and foraging under a high predation threat were measured. It was found that baboons preferred the low-risk, less profitable habitats and those outside their normal range for feeding and resting, and this was a conscious decision to minimise the risk of being killed by predators (Cowlishaw, 1997). Similar research by Caldwell (1986) found that after concerted predation by common black-hawks (*Buteogallus anthracinus*), heron species (*Ardeidae*) switched to poorer habitats, and foraged at dusk and during rainfall when predation was less risky, but the starvation threat increased. The trade-off between where species feed to maximise energy gain, whilst attempting to reduce the predation threat has also been recorded in numerous taxa: *e.g.* Butler *et al.* (2005) for chaffinches, Kotler *et al*. (1991) for gerbils (*Gerbillus allenbyi*), and Magnhagen (1988) for juvenile pink salmon (*O. gorbuscha*). The starvation-predation risk trade-off has been extensively studied in shorebirds by Barbosa (1997) (Dunlin), and for redshanks by Cresswell (1994b), Cresswell and Whitfield (1994), Hilton, Cresswell and Ruxton (1999), Hilton, Ruxton and Cresswell (1999), and Whitfield (2003).

Abiotic and biotic influences may impact upon both predation and starvation threat. For instance: high winds and low temperatures might increase both the energetic requirements of predators and prey; high tide height and time may affect the ability of coastal waders to forage, and high tides may restrict them to smaller foraging areas that increase their susceptibility to predation and starvation; and seasonal migration and return to breeding grounds may reduce numbers (and their availability for predators) and the ability to form larger (safer) flocks that can mitigate the predation threat (Lima and Dill, 1990; Mitchell *et al*., 2000; Yasue *et al*., 2003). Certain species of vegetation and vegetation structure (density and height) might provide better foraging areas for birds because prey are more numerous and likely to occur (Yasue *et al*., 2003). Contrastingly, denser and taller vegetation might hamper a bird's ability to forage, detect predators, and could provide a physical obstruction to flight escape as has been seen in other species such as chaffinches (Butler *et al.*, 2005), lapwings (Butler and Gillings, 2004) and Eurasian starlings (Whittingham and Evans, 2004). In this chapter, these influences will be evaluated to see how they affect the starvation-predation risk trade-off in redshanks.

Saltmarshes are known to be particularly important sites for redshanks, and their network of muddy creeks are an ideal feeding habitat for resident birds and Icelandic migrants which form around 50% of the British winter population (Prater, 1981). Besides offering redshanks access to preferred prey such as *Corophium*, *Nereis*, *Hydrobia* and *Macoma* (Goss-Custard, 1969), saltmarsh creeks may provide some protection from predation by raptors (Prater,1981). Nevertheless, on the rocky shore to the east of the study site in the winters of 1982/83 and

1983/84, mortality of redshanks caused by raptor predation was 20% and 16% respectively (Whitfield, 1985), much less than the 50% in winters 1989-1992, that was discovered on the saltmarsh by Cresswell and Whitfield (1994). It has been suggested that redshanks are therefore prioritising feeding on energetically beneficial *Orchestia* on the saltmarsh to avert the starvation risk, but at the expense of the predation risk (Cresswell, 1994a; Yasue *et al*., 2003; Minderman *et al*., 2006). Important abiotic and biotic factors influencing the trade-off are likely to be weather, tide, seasonal effects, prey availability and vegetation type and structure. Each of these may independently or interactively affect both the costs and benefits of feeding on the saltmarsh area at Tyninghame.

3.1.1 Abiotic influences on the distribution of redshanks

Weather conditions can affect redshank presence on the saltmarsh and regulate aspects of the starvation-predation risk trade off. High winds and low air temperatures increase the energetic costs of birds feeding in the open in habitats such as estuaries and mud flats, requiring them to prioritise starvation risk by relocating to sheltered areas (*e.g*. saltmarshes), but where the threat of predation may be greater (Lima and Dill, 1990; Mitchell *et al*., 2000; Yasue *et al*., 2003). Increased wind speed is particularly detrimental to survival, because it accelerates heat loss due to the forced convection of air moving over skin and feathers (Evans, 1976). For example, Gessaman (1973) found that in Snowy Owls (*Bubo scandiacus*), metabolic rate increased by 100% when wind speed rose from 0 to 9 m/s at temperatures of between -20°C and -30°C. In addition, it was found that after several days of strong winds, Grey Plovers' feeding technique was impaired because they were prevented from maintaining feeding position (Dugan *et al*., 1981). This might be relevant for species like redshank which feed by walking parallel to the tide edge, where a strong crosswind may increase instability, reducing their ability to feed efficiently, and increasing energetic costs (Evans, 1976). Strong winds may also conceal the sound of sandhopper movement, from *T. saltator* or *Orchestia,* which might otherwise act as a cue for foraging waders (Evans, 1976). Wind speed may also affect predators as well as prey, and Masman *et al.* (1986) indicated that energy demands for kestrels (*F. tinumculus*) increased in high winds. For long-eared owls (*Asio otus*), van Mannen (2001) found that an increase in energy demands in high winds, which resulted in a reduction in feeding success in the open, meant that the birds switched their hunting habitat to sheltered areas which altered their target prey from short-tailed vole (*Microtus arvalis*), to wood mouse (*Apodemus sylvestris*) and bank vole (*Myodes glareolus*). Lower soil temperatures may lead to invertebrate prey burrowing deeper and becoming less active in estuarine mud, which might make then less available and increase the starvation risk for wading birds (Goss-Custard, 1969; Evans, 1976; Yasue *et al*., 2003). Previous research in the study area by Hilton, Ruxton and Cresswell (1999) indicated that when this occurred, redshanks moved from the creeks onto the saltmarsh vegetation to feed.

Tidal constraints are also important in the starvation-predation risk trade-off. Because redshanks feed mainly by sight, they may have difficulty in reaching their required intake level when daytime high tides corral birds into less productive feeding areas (Prater, 1981). In particular, they may be more at risk of predation when high spring tides force them towards areas closer to predator-concealing cover. Night time feeding may allow redshanks to make up for any shortfall in their intake, although feeding by touch during darkness might not be as an effective technique as feeding by sight during daylight (Goss-Custard, 1969). The range of prey available may be dependent upon the point of the tidal cycle, because a neap tide results in fewer prey species being available for waders (Evans, 1976). Therefore, the height and time of the high tide may dictate if and how redshanks feed on

the saltmarsh, influencing their decision-making in compensating for starvation risk, possibly at the expense of a greater predation threat (Cresswell and Whitfield, 2008).

Seasonal population fluctuation of redshanks may confound the predictions of the starvation-predation risk trade-off in determining redshank use of the saltmarsh and foraging on *Orchestia*. Resident redshanks are found on estuaries in eastern Scotland throughout the year and their numbers are supplemented by Icelandic migrants, mainly juveniles, that begin to arrive in August and peak in September (Prater, 1981). Winter redshank numbers at Tyninghame probably vary on an annual basis and it appears that in recent years numbers over-wintering may have reduced from the totals observed in the early 1990s by Cresswell and Whitfield (1994). Similarly, their numbers throughout the winter may not be constant as birds arrive and leave Tyninghame estuary. There may be an onward migration which reduces numbers from October to December, although this may also be due to starvation mortality (Prater, 1981), which may be aggravated by shorter daylight hours which reduces feeding opportunities (Evans, 1976). However, Cresswell and Whitfield (1994) found that at the study site, there was very little mortality from September to March due to starvation, but density dependent mortality caused by raptors, of 31%, 48% and 57% occurred in winters 1989-1990, 1990-1991 and 1991/1992 respectively, particularly amongst first year juveniles which predominate on the saltmarsh. In eastern Scotland, numbers of redshanks increase slightly in January followed by a gradual decline until the end of March when Icelandic visitors return north (Prater, 1981). At the study site, feeding flocks can number up to about 100 birds earlier in the winter, but much smaller flocks of around 20 birds were seen on the saltmarsh by the end of March (Quinn and Cresswell, 2004). Therefore, there appears to be a fluctuation in numbers of redshanks at Tyninghame over the winter with the recruitment to the resident population of young Icelandic birds and passage migrants, that stopover during the early winter period before moving on.

3.1.2 The influence of vegetation on redshank distribution

A major biotic component of the starvation-predation risk trade-off will be prey availability: predators are more likely to be found, and may spend more time foraging, where prey density is greatest because these areas are more profitable (Royama, 1971). However, this is perhaps an over-simplistic assumption because at the highest prey densities there is a plateauing effect where feeding rate slows down and levels off, resulting in feeding time being more evenly distributed amongst patches (Royama, 1971). In addition, interference competition amongst predators at the highest prey densities results in them modifying their behaviour to reassess which areas are the most profitable. (Sutherland and Parker, 1998) It is therefore the amount of prey that can be eaten in a given time that is important to predators, and not necessarily foraging in the densest prey areas (Holling, 1959; Royama, 1971). Nevertheless, Goss-Custard (1980) suggested that waders are more likely to be found in areas of higher prey density, and subsequent research by (Goss-Custard, 1970a) in the Ythan estuary, northeast Scotland and by Goss-Custard *et al.* (1991) in the Severn estuary, southwest England, discovered that redshank numbers increased in conjunction with higher densities of *Corophium* and *N. diversicolor*. Although this was the general finding, it was discovered that in the *Corophium*-rich areas, there was mutual interference between birds which resulted in two effects where, 1) prey retreated further into their burrows - prey depression, and 2) redshanks mutually interfered with each other's feeding effort at higher bird densities, which meant that feeding efficiency was reduced. The author went on to say that prey depletion by a large flock might be countered by mutual interference

(Goss-Custard, 1970a). Depression of *Corophium* numbers by feeding redshanks has also been confirmed more recently by Stillman *et al*. (2000).

3.1.3 *Orchestia* density and redshank distribution

Evidence of redshanks feeding on *Orchestia*-dense areas was given by Goss-Custard and Jones (1976), where analysis of pellets showed that breeding redshanks exploited *Orchestia* (and *Corophium*) where these species were most abundant in the early summer. More recent research at the study site by Yasue *et al*. (2003) examined fauna from plots and found that 90% of invertebrate prey consisted of *Orchestia, Hydrobia* and *Littorina*, although *Orchestia* distribution on the saltmarsh was described as patchy. Redshanks were most likely to be found in areas where *Orchestia* density was high (56.4 ± 8.0 SE per m^2) and *Hydrobia* and *Littorina* densities were low (10.1 ± 4.4 SE per m^2). Foraging redshanks were therefore more likely to feed in denser areas of *Orchestia* (Yasue *et al*., 2003). However, there is a balance between predation risk and foraging in higher density *Orchestia* areas if this presents a greater threat. Cresswell (1994a) indicated that at the study site, juvenile redshanks were most likely to forage on the saltmarsh which was risk-prone, but where the profitability of feeding on *Orchestia* was greater than adjacent mussel beds, from where they were excluded by the adults. Although the threat of sparrowhawk attack was increased on the saltmarsh they benefited from a higher energy intake particularly in colder weather. Little work, however, has been undertaken to determine what species and composition of saltmarsh vegetation redshanks prefer to forage in when feeding on *Orchestia*. This is a crucial component to the starvation-predation risk hypothesis because vegetation will affect both the availability of *Orchestia* and the ability of redshanks to feed on *Orchestia* while maintaining their ability to detect and evade predators. Various authors have suggested that dense vegetation is necessary for *Orchestia* to reduce desiccation (Pomeroy, 1959; Colombini *et al.*, 2013) and provide shelter from predators (Kraeuter and Wolf, 1974; Colombini *et al.*, 2013). At the study site, Yasue *et al*. (2003) indicated that high *Orchestia* densities were found in *S. europaea* habitat where redshanks were also most likely to feed. Furthermore, saltmarsh grass adjacent to creek edges was preferred by feeding redshanks and held larger *Orchestia* of 11 to 15mm. This grass consists of two species, with *F. rubra* the most common in the outer marsh and *P. maritima* found mainly in the mid and inner marsh. Redshanks also foraged on *Orchestia* and probably *Hydrobia* found in *Pelvetia canaliculata* that had been deposited by high tides (Hilton, Ruxton and Cresswell, 1999; Yasue *et al*., 2003). Their feeding preference for specific patches of vegetation is an important consideration because species of vegetation might determine *Orchestia* species, size and density.

As well as vegetation type, its structure is important because this will affect how easily prey may be detected and how well it may allow prey to escape from the predator, as well as how the predator itself might detect and avoid predation from its predators (*e.g*. sparrowhawks in the case of redshanks) at a higher trophic level. Redshanks may concentrate their feeding in denser vegetation if *Orchestia* are more likely to be present and more abundant, but this may have its disadvantages. Research into set-aside land for granivorous birds by Clarke *et al.* (1997) found that as vegetation density increased, feeding efficiency reduced because birds were anxious about the predation threat due to greater difficulty in detecting predators. Sansom *et al*. (2009) found at the study site, that redshanks feed more intently in denser grass with their heads down, and that this might limit their awareness of the predation threat. Feeding in wet tall and dense vegetation in winter might also wet plumage and lead to increased heat loss, besides restricting movement (Dawson *et al*., 1992; Clarke *et al.*, 1997). Detecting food items

in dense vegetation might prove more difficult especially if the prey is cryptic (Butler and Gillings, 2004; Whittingham and Evans, 2004) and where the complex structure and shininess of the grass sward increases scanning time (Whittingham and Markland, 2002). Furthermore, increased vegetation height might affect redshank feeding, in a similar way to that of increased density of the sward. Research by Butler *et al.* (2005) investigated stubble heights and found that chaffinches perceived that foraging in higher stubble obstructed vision and inhibited detection of predators. It is suggested that in shorter vegetation, a reduced need for vigilance improved the foraging efficiency of 11 of the 20 species that are part of the Government's Farmland Bird Index, used to assess the value of wildlife in farming systems (Whittingham and Evans, 2004). Butler and Gillings (2004) mention that foraging efficiency declines in the case of lapwings when higher vegetation interferes with the bird's ability to sight prey and restricts mobility, which was also found in Eurasian starlings by Whittingham and Evans (2004). Foraging was discovered to be 33.2% more profitable for starlings feeding on invertebrates on the surface and in the subsurface of soil in shorter vegetation, and this profitability decreased as the vegetation got taller (Devereux *et al*., 2004). A mosaic of diverse patch heights may provide benefits for invertebrates that are able to shelter in taller vegetation, but also their predators which prefer to forage and disperse (so reducing interference with conspecifics) in areas of shorter vegetation (Benton *et al*., 2003).

3.1.4 Objectives

This chapter will investigate the presence of redshanks on the saltmarsh and what influences their decision to feed there, in terms of abiotic and biotic predictors.

14. Although previous research at the study site suggests that when foraging on the saltmarsh redshanks are primarily taking *Orchestia*, this part of the research will confirm this. Therefore, any gizzards discarded by sparrowhawks or remains from interrupted kills will be dissected. The hypothesis is that redshanks on the saltmarsh feed on *Orchestia*.

15. Season. Differences in redshank presence will be investigated throughout the winter period. The hypothesis is that, because starvation risk increases for redshanks in winter, presence on the saltmarsh will increase from late Autumn until January and February, before declining in March when visiting winter birds return to their summer breeding grounds.

16. Weather. The prediction is that the probability of redshank presence will increase as temperatures become colder and wind speed increases, because in these conditions starvation risk is greater and redshanks need to feed on more profitable *Orchestia* on the saltmarsh even though this results in a higher predation threat from sparrowhawks.

17. Tide (time to and from the nearest high tide and height of the nearest high tide). An assessment will be made on how redshank presence varies across the daily tidal cycle and the springs to neaps tidal range. It is expected that daily presence of redshanks on the saltmarsh will vary and will be dependent on the time of the high tide, although how this varies is unknown. Redshank presence should increase during spring tides when available saltmarsh foraging habitat is reduced.

18. *Orchestia* density. It is predicted that redshanks are more likely to forage in areas where *Orchestia* are most abundant.

19. Vegetation composition. Redshanks may feed in specific species of vegetation whilst avoiding others. It is predicted that they are more likely to occur in vegetation that gives them their highest intake from *Orchestia*.

20. Vegetation structure. The hypothesis is that redshanks will feed in less dense and shorter vegetation because this will reduce hindrance when foraging and allow them to better detect sparrowhawk attack.

3.2 Methods

3.2.1 Confirming that redshanks feed on *Orchestia*

To achieve objective 14 and confirm that redshanks were foraging primarily on *Orchestia*, it was hoped that discarded gizzards for dissection could be collected from sparrowhawk kills. In the event, only one bird was found from an interrupted kill witnessed in winter 2 (14 Jan 2015) at 56º01'18.39"N -2º59'38.633W. This was removed for dissection.

3.2.2 Measuring redshank feeding occurrence

Redshank feeding occurrence was evaluated in winters 2 and 3. A Leica 20-60x zoom 80mm spotting scope was used to identify feeding redshanks from distances of >70m. The flock positions of the lead bird, then bird 5, and then every fifth bird (*i.e*. bird 10, 15, 20 etc.), were estimated and recorded with the handheld GPS. The position of waymark points (*e.g*. trees, bends in creeks, branches embedded in the marsh) had been previously uploaded onto the GPS to enable a more accurate estimation of bird position. Redshank observations were entered into ArcGIS software (ESRI, 2013) and from these an isopleth map was produced of redshank feeding density on the saltmarsh (Figure 3.1). Method: Geoprocessing > Environment > Processing Extent > Raster Analysis > Tools > Point Density. Settings: Layer Properties = Classification, Breaks = 13, Natural Breaks (Jenks), Display = Bilinear Interpolation for Continuous Data.

Feeding presence in relation to season, weather and tide

Objectives 15 – 17. Redshanks were categorised as present - feeding for some part of the day on the saltmarsh, or absent - feeding elsewhere (*e.g*. creeks, the rocky shore to the east, or the estuary). There were 40 fieldwork days in winter 2 and 40 in winter 3. Date was aligned with the fieldwork period in winter 1, where day 1 was 11 Nov and the last day, 141, as 31 Mar. Weather conditions were measured at three positions on the saltmarsh: A. 56°015'N, 2.591'W (north); B. 56°011'N, 2°588'W (southeast); C. 56°012'N, 2°594'W (west). Air and wind speed readings were taken at these positions using the handheld mini weather station, and soil temperatures using the laboratory thermometer and probe to a depth of 1cm. The average of each reading was then calculated to give a daily value for the saltmarsh. Times and heights of high tides were taken from Dunbar. No observations were recorded one hour either side of high tide because of the certainty of redshank presence on the saltmarsh during these periods when all other areas were flooded. Numbers of *Orchestia* were categorised as either 1 – present, or 0 - absent, and initially processed in a GLM with a binomial distribution (Bernoulli GLM) as was done for *Orchestia*. The default logit link function was used initially, but this was subsequently changed to probit because this produced better models (Thomas *et al.*, 2015).

Analysis with non-parametric, smoothed variables

Another way of testing the data was to use a generalised additive model (GAM). A GAM displays non-parametric smoothed lines of best fit through a dataset (Zuur *et al.*, 2009; Fridley, 2010; Thomas *et al*., 2015). The package used was mgcv (Wood, 2011). Although a GAM uses more degrees of freedom than a GLM, the penalty may not be a problem if the dataset is large. This was the case when this method was used for presence/absence models

of redshanks on the saltmarsh which had 80 cases. Also, a GAM could be compared to an equivalent GLM by using AIC or by running an ANOVA, which determines the best model structure (Fridley, 2010; Thomas *et al*., 2015). In this case, day number was entered as a non-parametric smoothed continuous variable in the GAM which maximised the goodness of fit (Wood, 2011). The GAM produced a better model when compared to the equivalent GLM.

3.2.3 Feeding distribution and *Orchestia* density

Objective 18 predicted that redshanks were more likely to forage in the densest *Orchestia* patches. A preliminary visualisation was produced by creating an isopleth map for the density of each *Orchestia* species based on the distribution data from winter 1, using ArcGIS software (ESRI, 2013), as the procedure in 3.2.2. Eight levels of *Orchestia* density were configured (*natural Jenks* setting), so that 1 was the least dense and 8 the densest. Redshank observation points from winters 2 and 3 could then be overlaid on top of this (Figure 3.3, page 90). The isopleth map in Figure 3.1 was then utilised to constructed binomial GLMs by using the 13 redshank feeding areas graded from area 0 = no redshanks present, up to area 12 where redshanks were densest. These areas were then reconfigured for a binomial GLM where 0 = redshanks absent and levels 1-12 = redshanks present. GLMs were then run separately for each *Orchestia* species which were entered as the predictor variable, and the probability of redshank presence as the response variable. Winter was also added to the models as a confounding variable.

3.2.4 Vegetation composition in feeding areas

To complete objective 19, initial investigation was conducted by non-metric multidimensional scaling (NMDS) using the Ecodist package (Goslee and Urban, 2007) to give an overview of whether species of vegetation could be attributed to redshank feeding and/or non-feeding areas. Information was recorded from 1m x 1m plots in winters 2 and 3, immediately after redshanks had been disturbed from feeding on them. These were compared against 1m x 1m plots from non-feeding areas selected at random, where these data were gathered as part of other experiments. Binomial models were then constructed using the same data where plot type was the response variable and species of vegetation the predictor. Winters 2 and 3 were modelled together, but winter was added to the models as a confounding variable.

3.2.5 Vegetation structure in feeding areas

Overall vegetation density, height and highest vegetation data taken from plots in in redshank feeding and non-feeding areas was investigated in winter 2 separately to the composition of vegetation in 3.2.4. Using ArcGIS software (ESRI, 2013) bimodal areas were constructed for redshank feeding density. Therefore, new polygons were digitised from the redshank feeding density isopleth map (Figure 3.1) where the highest feeding density areas 4 to 13 were designated as feeding areas, and the lowest densities 1 to 3 as non-feeding areas. One hundred random points were then generated, 49 in feeding areas and 51 in non-feeding areas, and uploaded onto the handheld GPS, so that these plots could be visited and measurements taken. Overall density was the estimated ground cover in a 1m x 1m quadrat, height was the average height of the 4 corners and its centre, and highest measured the tallest vegetation in the plot. A binomial GLM was used to model the data.

3.3 Results

3.3.1 Analysis of redshank gizzard contents – objective 14

The gizzard contents of a redshank found from an interrupted kill in winter 2 (15 Jan 2015) were examined (Table 3.1).

Table 3.1 *Redshank gizzard contents from an interrupted sparrowhawk kill recovered in winter 2.*

Ser No	Description	Number
1	*Orchestia* leg	8
2	*Orchestia* flagella	5
3	*Orchestia* coxal plates	7
4	Cestode parasite, or *Orchestia* ventral nerve cord	37
5	*Orchestia* gnathopod	2
6	*Orchestia* whole	1 *O. mediterranea*, 1 *O. gammarellus*
7	*Hydrobia* whole	30
8	Other gastropods	2
9	Shell fragments including inner spires	Many

Besides numerous *Orchestia* fragments there were two whole *Orchestia* (between 8 and 10mm in length), and 37 ribbon-like white threads that had not passed into the intestine. There were also many *Hydrobia* both whole (all <1mm) and fragmented. The hypothesis in objective 14 is supported, in that when foraging on the saltmarsh, redshanks feed on *Orchestia*.

3.3.2 Redshank feeding presence on the saltmarsh – objectives 15-18

Feeding flock sizes were larger in winter 2 compared to winter 3 (Table 3.2). Flocks in winter 2 fed over a greater range, mainly at the western edge and around the northern tip of the saltmarsh on *A. maritima* and *F. rubra*. They began to feed on the saltmarsh in the second week in November and were there for the duration of the winter until the first week in March. A flock was also observed feeding on the south east of the saltmarsh during the first week of February to the west of Sandy Hirst, on scattered *P. maritima* tussocks. In winter 3, flocks of fewer birds began feeding intermittently on the saltmarsh in the third week of November for two weeks until the beginning of December, and then again from the third week of January until the second week of March. The main feeding was concentrated to the north west of the saltmarsh close to the *Phragmites australis*, reed bed and stretching northwards across patches of *A. maritima* and *F. rubra* redshank occurrence maps for each winter are shown in Figure 3.1. The data concerning presence and absence of feeding redshanks is also shown in Table 3.2.

Table 3.2 *Data for redshank observations in winters 2 and 3.*

	No of redshanks observed in total	Mean birds per observation	SE
Observation recordings winter 2 = 200	3509	17.55	0.61
Observation recordings winter 3 = 115	540	4.66	0.24

Variable measured	Days present = 40	Mean	SE
High tide height (m)		4.77	0.08
High tide time (decimal hrs)		11.76	0.53
Air temperature (ºC)		5.22	0.41
Soil temperature (ºC)		4.58	0.40
Wind speed (mph)		3.43	0.57
	Days absent = 40	Mean	SE
High tide height (m)		4.96	0.07
High tide time (decimal hrs)		9.77	0.65
Air temperature (ºC)		6.78	0.44
Soil temperature (ºC)		7.03	0.36
Wind speed (mph)		5.76	0.62

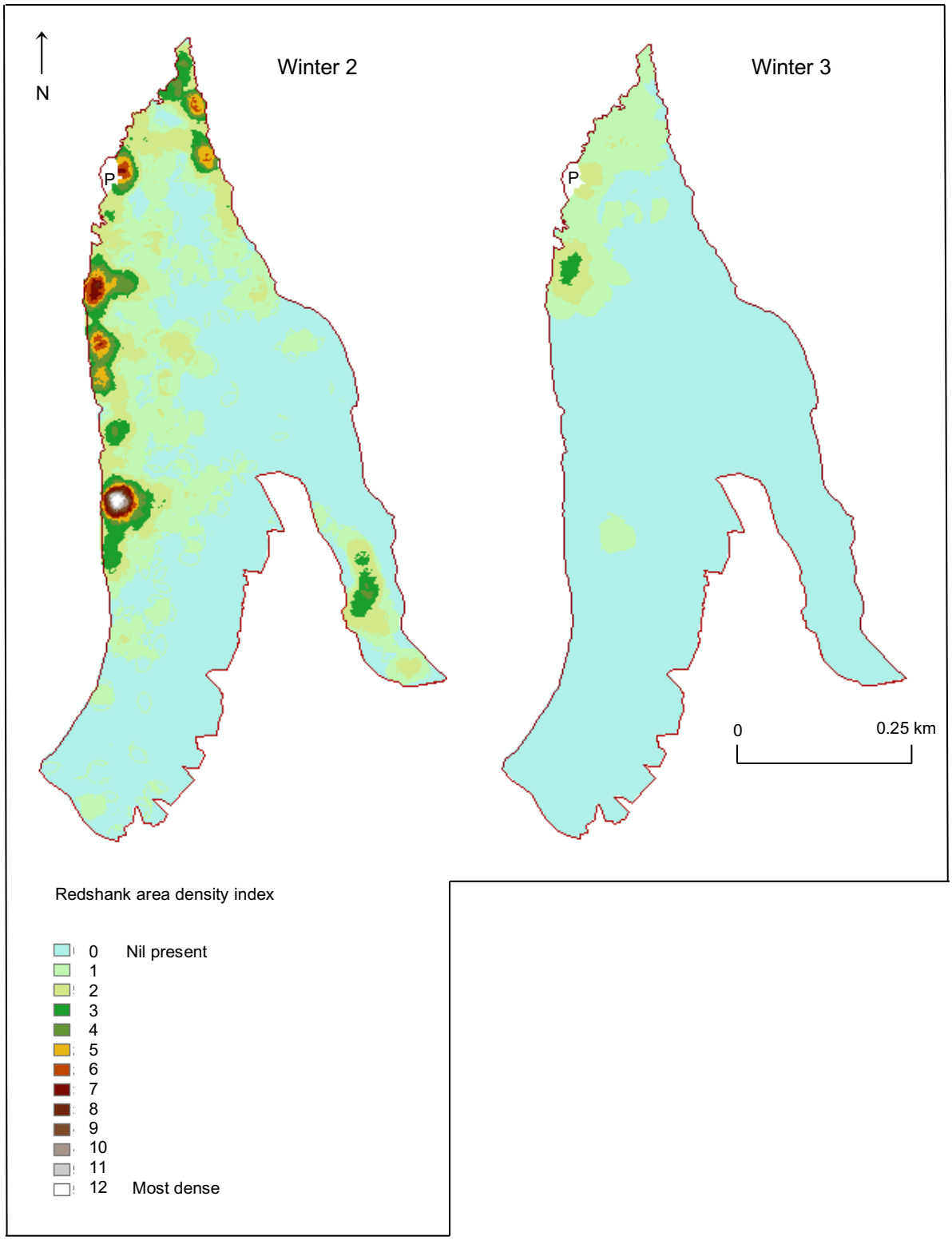


Figure 3.1 *Redshank density map, showing feeding density for winters 2 and 3. This is an arbitrary index of feeding density configured in ArcGIS, where 0 = no birds feeding and 12 = highest density of birds feeding. P is an area of the land-based grass Poa (species not known) which encroaches onto the saltmarsh and makes the area unavailable for redshank feeding because of its dense structure.*

The best probability model for redshank feeding presence was a GAM with a binomial distribution, which produced an AIC of 59 where a non-parametric curve with a smoothing function was applied to day number using

automatic knot selection which in this case produced 4 knots in the fitted line. This compared to an AIC of 67 for the best binomial GLM in which day number was entered as a quadratic effect (Table 3.3).

Table 3.3 *Redshank feeding presence showing results of the best GAM with a binomial distribution. Day number was entered with a smoothing function.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	8.46	2.78	3.0	0.002
Soil temperature	-0.29	0.12	-2.4	0.016
Time of nearest high tide (hrs)	0.20	0.08	2.5	0.014
Nearest high tide height (m)	-1.90	0.62	-3.1	0.002
Smoothed variable	edf	ref.df	X^2	
Day number	4.99	6.11	17.3	0.009

All *P* values significant. The pseudo R^2 for this model is 0.63. Degrees of freedom 76. Best model AIC: 59, full model AIC: 70, best GLM AIC: 67. Variables removed from full model: air temperature, year and wind speed.

Seasonal variation - objective 15

By smoothing the day number predictor variable in the GAM, a more accurate indication was given of redshank presence on the saltmarsh throughout the winter. The probability of occurrence dipped between autumn and early January where this reduced from 0.34 to 0.11. There was then an increase in the likelihood of redshanks feeding on the saltmarsh to a probability of 0.79 in mid-February before reducing again to 0.12 by the end of March. Therefore, although the hypothesis that redshank presence increases on the saltmarsh from late autumn before decreasing in early spring is correct, there is a period around November when they are less likely to be present on the saltmarsh.

Weather - objective 16

Soil temperature indicated a significant effect and showed a negative relationship where the probability that feeding birds were on the saltmarsh was 0.94 at 0°C compared to 0.32 at 12.5°C. The other predictor variables associated with weather, air temperature and wind speed, were removed from the best model due to having no significant effect. This indicates that the prediction that redshanks are more likely to feed on the saltmarsh at lower temperatures is partly supported where only soil temperature is a variable, not air temperature. In addition, an increase in wind speed was not indicative of the presence of feeding redshanks.

Tide - objective 17

The time of high tide was also significant and showed a positive relationship with an increase in the probability of feeding birds being present of 0.08 when the nearest high tide was at 0300 hrs up to 0.65 at 1630 hrs. The height of the nearest high tide showed a significant negative relationship and a decrease in the probability of redshank presence from 0.95 at a high tide of 4 m down to a probability of 0.33 when the high tide was at 5.9 m (Table 3.3, Figure 3.2). Therefore, although redshanks were more likely to forage when a high tide was in the afternoon, the prediction that they are more likely to be present when areas of available foraging on the saltmarsh are reduced due to high spring tides was not proven. In fact, they were more likely to feed on the saltmarsh during low neap high tides which do not flood above creek level.

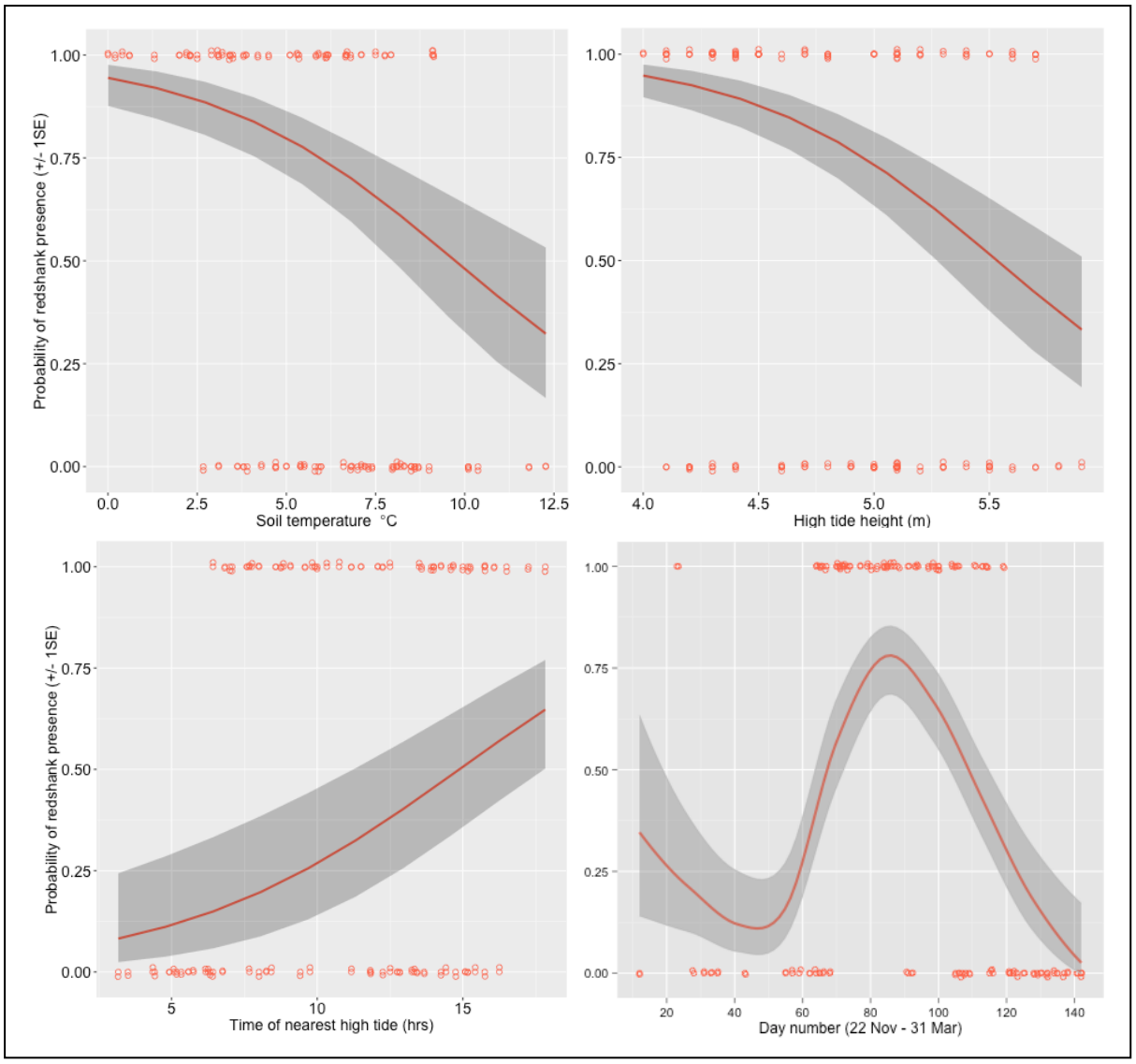


Figure 3.2 *Redshank feeding presence probability predictions for soil temperature (top left), tide (top right, bottom left) and the smoothed fit for day number with observations starting 22 November (bottom right). Parameter estimates and SEs plotted from the model in Table 3.3. Jittering was used for clarity, to disperse points of equal value.*

Orchestia density – objective 18

When redshank feeding flock observations for winters 2 and 3 were initially plotted on an *Orchestia* density isopleth map, in general there appeared to be little similarity between areas of highest feeding flock density and highest *Orchestia* density (Figure 3.3). Models were then constructed using Figure 3.1 for each *Orchestia* species to determine the relationship between redshank presence and *Orchestia* abundance. The data for these models are in Table 3.4.

Table 3.4 *Data for redshank feeding density occurrence from 13 areas (0 = absent, 1-12 = present) in winters 2 and 3 against Orchestia abundance in winter 1.*

	Winter 2			Winter 3		
O. gammarellus	*N*	Mean	SE	*N*	Mean	SE
Absent – redshank feeding area 0	139	0.46	0.09	422	0.88	0.16
Present – redshank feeding areas 1-12	428	1.73	0.32	270	2.32	0.36
O. mediterranea						
Absent – redshank feeding area 0	832	1.75	0.16	501	1.69	0.21
Present – redshank feeding areas 1-12	109	1.01	0.29	292	1.5	0.20

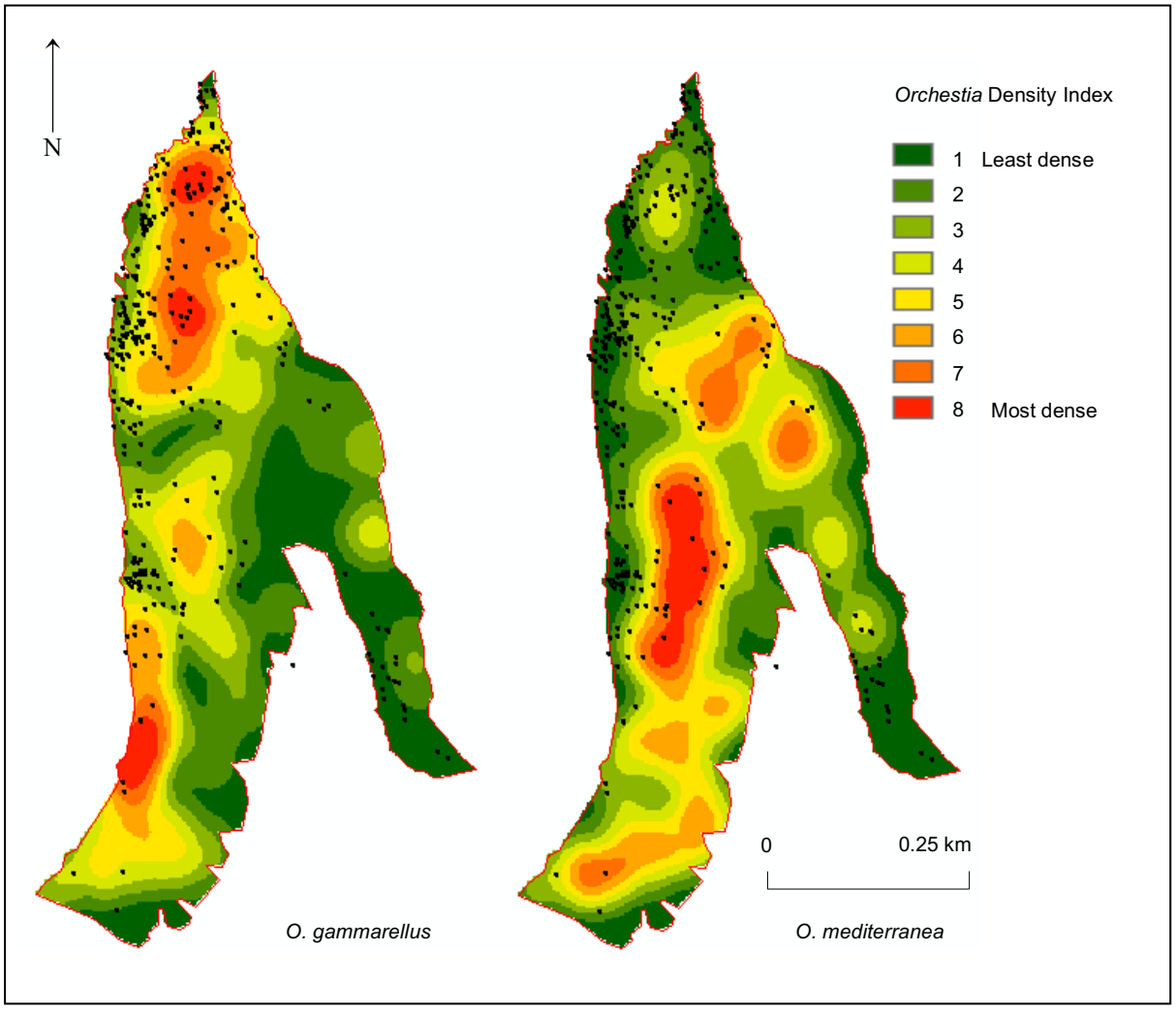


Figure 3.3 *Redshank feeding flock observations shown as lead bird (black dots) for winters 2 and 3 combined (n = 317 flock observations), on an isopleth map of Orchestia density (Orchestia data from winter 1). The Orchestia density index is split into 8 levels, with 1 being the least dense area of Orchestia and 8 being the densest. Table 4.2 and 4.3 refer.*

Orchestia gammarellus

The best GLM with a binomial distribution for the probability of feeding redshank presence, showed a significant positive quadratic effect when related to *O. gammarellus* abundance of between a minimum of 0 and maximum

of 17 individuals. This was true for both winters 2 and 3, but the probability of redshank feeding presence was greater during winter 2 where the probability of redshank occurrence increased along with *O. gammarellus* abundance from 0.39 where *O. gammarellus* was absent, up to 0.84 at around 12 individuals, before decreasing again slightly to 0.78. This compared to winter 3 where the probability of redshank presence was 0.09 up to 0.44 reducing to 0.37 across the same *O. gammarellus* abundance range (Table 3.5, Figure 3.4).

Table 3.5 *Best GLM binomial model for redshank feeding presence for O. gammarellus. An area density index was used to categorise redshanks as present (areas 1-12) or absent (area 0) using redshank feeding data from winters 2 and 3.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	-0.44	0.09	-4.66	**0.001**
O. gammarellus	0.34	0.07	4.72	**0.001**
O. gammarellus^2	-0.01	0.01	-2.47	**0.013**
Winter 3	-1.87	0.16	-11.29	**0.001**

All P values were significant. The pseudo R^2 for this model is 0.15. Degrees of freedom 1081. Full model AIC: 1104, best model AIC: 1100. Variables removed from full model: O. gammarellus*winter and O. gammarellus^2*winter.

Orchestia mediterranea

The best GLM comparing redshank presence to *O. mediterranea* abundance (min 0, max 32) showed no significant effect when *O. mediterranea* was entered as a single variable. However, as an interaction with winter there was a significant negative relationship for winter 3 only, where the probability of redshanks being present reduced from 0.14 in plots containing no *O. mediterranea* to almost zero when abundance was 15. Therefore, the probability of occurrence of redshanks appears to very low in *O. mediterranea* habitat (Table 3.6, Figure 3.4).

Table 3.6 *Best GLM binomial model for redshank feeding presence for O. mediterranea. An area density index was used to categorise redshanks as present (areas 1-12) or absent (area 0) using redshank feeding data from winters 2 and 3.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	-0.20	0.10	-2.1	**0.035**
O. mediterranea	0.01	0.03	-0.2	0.844
Winter 3	-1.59	0.18	-9.0	**0.001**
*O. mediterranea**Winter 3	-0.23	0.10	-2.4	**0.017**

Significant *P* values are marked in bold. The pseudo R^2 for this model is 0.13. Degrees of freedom 1069. Full model AIC: 1120, best model AIC: 1116. Variables removed from full model: *O. mediterranea*^{2} and *O. mediterranea*^{2}*winter.

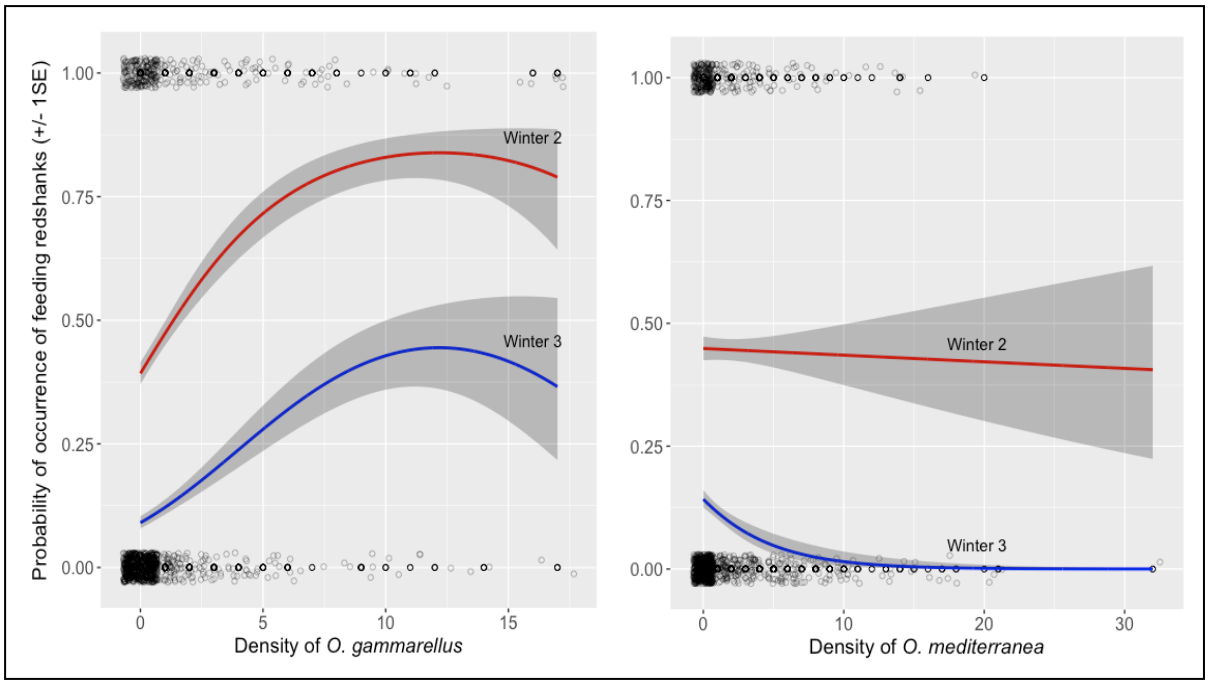


Figure 3.4 *The probability of redshank feeding presence for winters 2 and 3 compared to Orchestia density from winter 1. Left - O. gammarellus, right - O. mediterranea (marginal non-significant effect). From the best GLM with a binomial distribution where Orchestia were counted from 700 plots from winter 1 and compared with feeding redshank observations in winters 2 and 3. Redshank data were plotted in ArcGIS and given a density area index score from 0-12: 0 = nil redshanks, 12 = highest density (Figure 3.1). This was then converted to binomial present/absent data for modelling (i.e. 0 = redshanks absent, 1 (0-12) = redshanks present). Parameter estimates and SEs plotted from the models in Tables 3.5 and 3.6.*

Therefore, the results suggest that redshanks were more likely to forage on *O. gammarellus* when abundance increased, but were then less likely to forage on this species when it was at the highest densities. In contrast, redshanks appeared to avoid *O. mediterranea* because results indicate that there was no significant relationship between redshank occurrence and increased *O. mediterranea* abundance in winter 2, and a low probability of occurrence in winter 3, in areas that had higher abundance. This would suggest that the prediction that redshanks feed in areas of higher *Orchestia* density is more complex than first realised and other factors must impact upon a redshank's ability to feed in the most profitable areas.

3.3.3 Vegetation in redshank feeding areas - objectives 19 and 20

The data for vegetation composition in 404 feeding and non-feeding plots in winters 2 and 3, are shown in Table 3.7.

Table 3.7 *Species of vegetation coverage data for 404 feeding and non-feeding plots sampled in winters 2 and 3.*

	Winter 2				Winter 3			
	Feed = 26 plots		Non-feed = 180 plots		Feed = 45 plots		Non-feed = 153 plots	
Species	Mean coverage (%)	SE	Mean coverage (%)	SE	Mean coverage (%)	SE	Mean coverage (%)	SE
F. rubra	13.85	5.94	15.81	2.33	27.60	5.66	15.54	2.47
A. maritima	30.77	5.44	14.31	1.73	30.11	4.02	16.52	2.03
P. maritima	31.65	5.25	28.23	2.26	22.64	4.54	31.46	2.87
Pl. maritima	1.42	0.50	1.76	0.48	1.24	0.26	0.84	0.19
S. europaea	0.58	0.42	2.85	0.44	0.76	0.23	1.63	0.32
S. maritima	0.38	0.27	0.96	0.21	0.20	0.13	0.46	0.14
A. tripolium	2.42	0.88	1.46	0.30	1.38	0.36	1.69	0.29

Vegetation composition – objective 19

Initial investigation of dissimilarity based analysis using NMDS plots for redshank feeding and non-feeding areas related to vegetation composition were constructed for winters 2 and 3. There were some similarities in the spatial separation of species of vegetation, where some plants such as *P. maritima*, *A. maritima* and *F. rubra* were distinct from the other saltmarsh species. In winter 2, the visualisation gave little information about which species occurred where, except that *P. maritima* was more associated with non-feeding areas. In winter 3 this trend was repeated. *Pl. maritima* and plants of the inner saltmarsh such as *A. tripolium*, *S. europaea* and *S. maritima* were associated with non-feeding areas in winter 2, whereas in winter 3 the occurrence of these species was more confused where they were associated with both feeding and non-feeding areas (Figure 3.5).

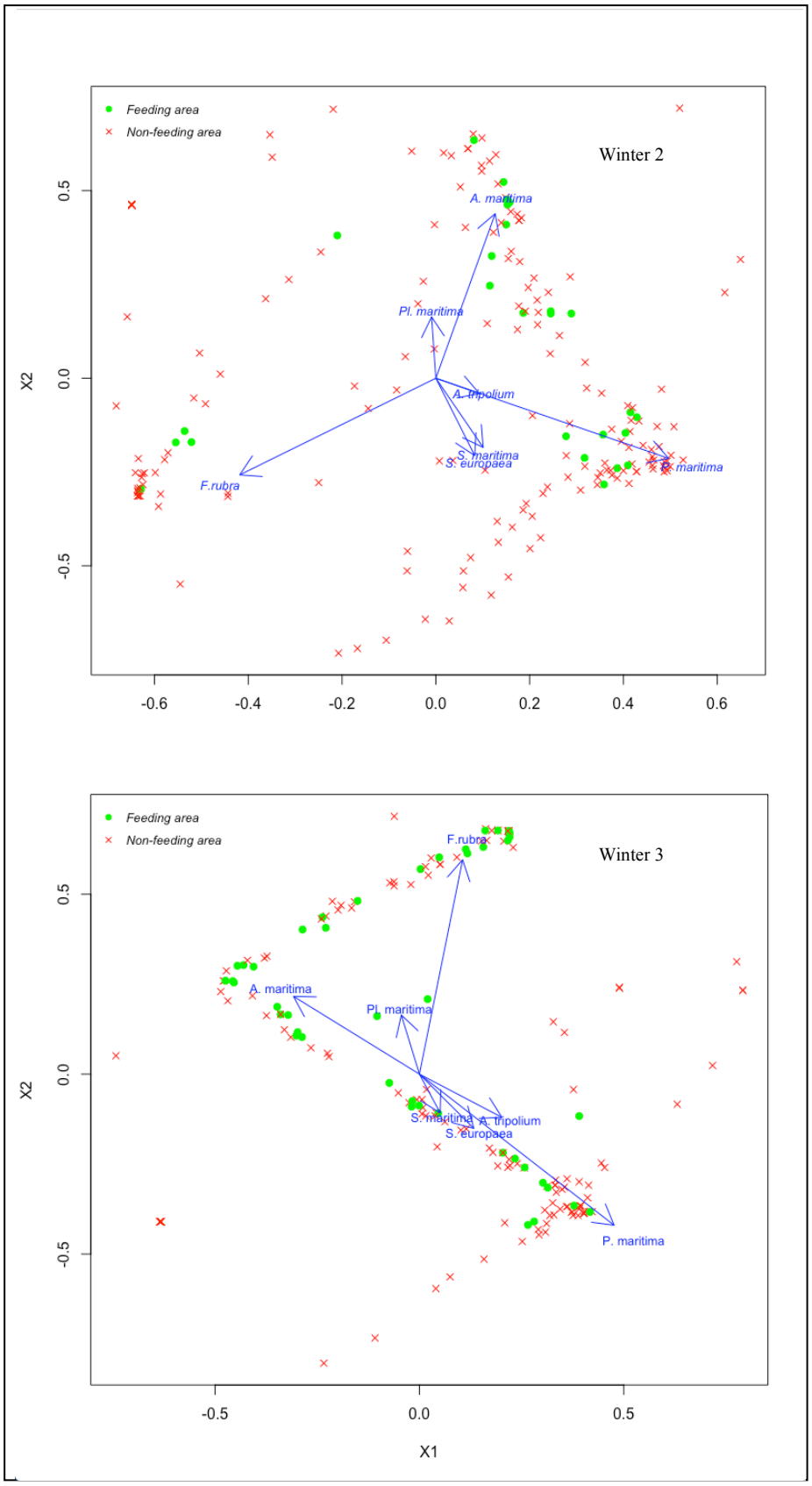


Figure 3.5 *NMDS scaling diagram showing species of vegetation and their separation distances in 2-dimensional space relating to redshank feeding and non-feeding areas, for winter 2 (top) and 3 (below).*

A binomial GLM was used to determine the probability that species of vegetation were associated with redshank feeding areas. The probability of redshank occurrence was greatest in *A. maritima* and at 95% coverage this was 0.47 in winter 2 and 0.61 in winter 3, but only 0.05 and 0.09 when *A. maritima* was absent. When *F. rubra* was at 100% coverage the probability was 0.23 in winter 2 and 3.9 in winter 3, compared to when this grass was absent from the sward - probability 0.05 in winter 2 and 0.09 in winter 3. The probability of redshanks feeding in *P. maritima* was less pronounced with a probability of 0.15 and 0.24 at 100% coverage, and 0.05 and 0.08 when the grass was absent, for winters 2 and 3 respectively. For *S. europaea*, the probability of redshank feeding occurrence showed a marginally non-significant effect, of little biological significance, equalling 0.05 (winter 2) and 0.09 (winter 3) when the plant was not present, down to almost zero probability at 40% coverage (Table 3.8, Figure 3.6).

Table 3.8 *Best binomial GLM for the probability of species of vegetation occurring in redshank feeding areas.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept (includes Winter 2)	-3.06	0.45	-6.7	**<0.001**
Winter 3	0.57	0.28	2.0	**0.043**
A. maritima	0.03	0.01	4.4	**<0.001**
F. rubra	0.02	0.01	2.8	**0.005**
P. maritima	0.01	0.01	2.1	**0.034**
S. europaea	-1.13	0.07	-1.7	0.084

Significant *P* values are marked in bold. The pseudo R^2 for this model is 0.18. Degrees of freedom 403. Full model AIC: 355, best model AIC: 348. Number of correct classifications = 0.82%. Variables removed from full models: Winter**F. rubra*, Winter**A. maritima*, Winter**Pl. maritima*, Winter**P. maritima*, Winter**S. europaea*, Winter**A. tripolium*, *Pl. maritima*, *A. tripolium, S. maritima*.

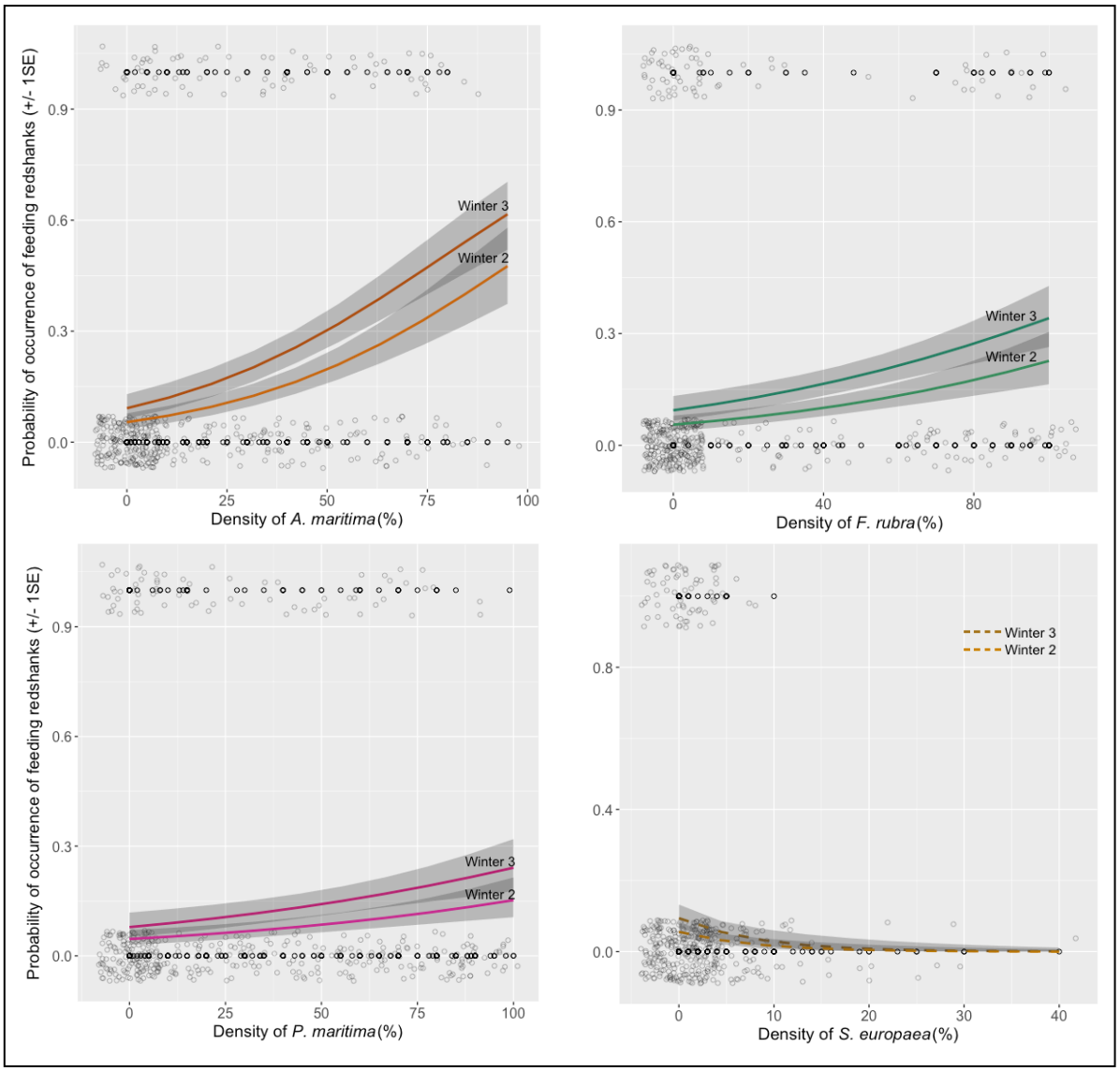


Figure 3.6 *Probability of occurrence of feeding redshanks in 4 species of vegetation from the best binomial model. F. rubra (top left), A. maritima (top right), P. maritima (bottom left), and S. europaea (bottom right), which showed a marginal non-significant effect. Probability of occurrence was significantly greater in winter 3 compared to winter 2. Parameter estimates and SEs plotted from the model in Table 3.8. Jittering of points used for clarity.*

Vegetation structure – objective 20

A binomial GLM was used to determine if redshank foraging was more likely to occur in different vegetation densities, but vegetation density was removed from the model because it showed no significant effect. However, mean vegetation height did show a significant effect where the probability of feeding redshanks decreased from 0.85 at 8mm down to a probability of 0.03 when mean vegetation height was 135mm. The highest vegetation in a sample plot was also measured, but this was also removed from the model as it showed no significant effect (Table 3.10, Figure 3.7). Therefore, the only hypothesis that was proven regarding vegetation structure is that redshanks are more likely to feed in shorter vegetation.

Table 3.9 *Data for vegetation structure in redshank feeding and non-feeding areas*

	Vegetation density		Vegetation height		Highest vegetation	
	Mean	SE	Mean	SE	Mean	SE
Redshank feeding area	88.75	1.35	36.77	3.50	149.27	5.80
Redshank non-feeding area	89.55	1.87	64.23	3.86	175.43	6.62

Table 3.10 *Height of vegetation in redshank feeding areas, the only significant variable in the best model for vegetation structure when redshank feeding areas were compared to non-feeding areas.*

Variable	Estimate (Log)	SE (Log)	*z*	*P*
Intercept	2.09	0.53	3.9	**<0.001**
Height	-0.04	0.01	-4.2	**<0.001**

All *P* values were significant in the best model. Degrees of freedom 94. Number of correct classifications = 0.76%. The pseudo R^2 for this model is 0.18. Full model AIC: 116, best model AIC: 111. Variables removed from full model: height*highest, vegetation density*height, vegetation density*highest, highest, vegetation density.

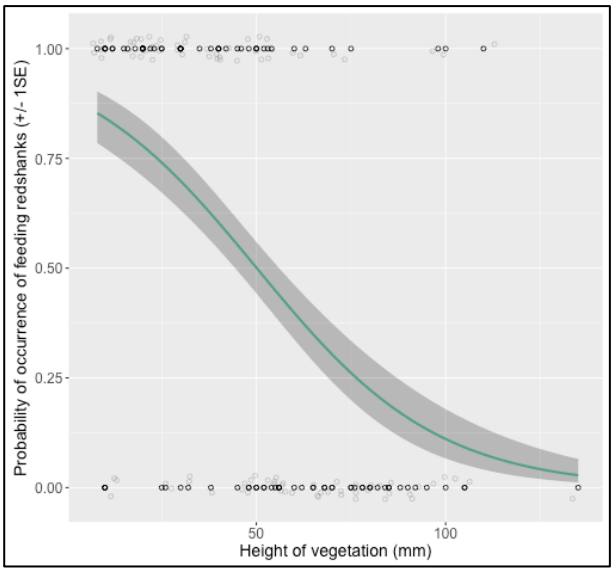


Figure 3.7 *Height of vegetation and the probability of occurrence of feeding redshanks. Parameter estimates and SEs plotted from the model in Table 3.10. Jittering is used for clarity.*

3.3.4 Summary of results

Dissection of a gizzard from a redshank attacked and killed by a sparrowhawk confirmed that redshanks foraging in saltmarsh vegetation feed on *Orchestia*, but also *Hydrobia*. This bird also appeared to be parasitized by cestode worms.

The presence of redshanks on the saltmarsh was evaluated against several parameters. Smoothing the day parameter in the model indicated that there was a dip in the probability of redshanks occurring on the saltmarsh between autumn and early January, but this increased after mid-winter, again followed by a decrease in early spring. The only weather variable that had a significant effect on redshank presence was soil temperature where birds were more likely to forage on the saltmarsh when this was at freezing point compared to higher soil temperatures. Redshank presence increased when high tides were in the afternoon, but decreased during spring tides when high tides are higher.

Redshank presence was also measured in relation to *Orchestia* density and although it was expected that occurrence of feeding redshanks should be more likely in areas of higher *Orchestia* abundance, this was not necessarily the case. Redshank presence probability increased in line with *O. gammarellus* abundance but then this tailed off in the densest areas of *O. gammarellus*. Moreover, redshanks appeared to avoid feeding in *O. mediterranea* areas as there was no significant effect in winter 2 of an increase or decrease in the probability of redshank occurrence in areas of higher *O. mediterranea* abundance. Although this presence probability showed a significant decrease in areas of higher *O. mediterranea* density in winter 3, this was a very small effect.

Redshank presence when related to the density of individual species of vegetation resulted in a significant effect for three species of vegetation, *A. maritima*, *F. rubra* and *P. maritima*, and redshanks were more likely to be present when the density of these species increased. The greatest effect was for the first two, species associated with the outer saltmarsh. The overall density of the sward had no significant effect on redshank feeding presence, but they were more likely to forage in shorter vegetation.

3.4 Discussion

3.4.1 Redshank diet when feeding in saltmarsh vegetation

The contents of the redshank gizzard that was dissected contained very small *Hydrobia* and shell parts, and whole and fragmented *Orchestia*. Cresswell (1994a) witnessed redshanks feeding on *Hydrobia*, and they were also found to be a component of redshank pellets by Goss-Custard and Jones (1976). Lourenço *et al*. (2017) indicated that in the Bajagós archipelago, Guinea-Bissau, redshanks droppings only consisted of low proportions of *Hydrobia* (0.01 of the biomass of droppings, $N = 25$), whilst at the study site, Yasue *et al*. (2003) suggested that redshanks were taking *Hydrobia* infrequently because they were at low densities (10.1 ±4.4 (SE) per m^2). An explanation might be given by De Vlaming and Proctor (1968) where it was discovered that plastic markers used to simulate propagule digestive time in killdeer (*Charadrius vociferous*) and mallard ducks (*Anas platyrhynchos*) often remained trapped in the digestive system, particularly the gizzard. Likewise, Mateo *et al*. (2000) indicated that for ducks and coots, shot pellets, rice and other small hard objects were used as grit to aid digestion. Therefore, it might be that *Hydrobia* are retained for such a purpose and that they have a longer residence time in the gizzard. This is supported by observations which suggest that *Hydrobia* are patchy in distribution, their main habitat being on the south-eastern saltmarsh adjacent to Sandy Hirst in more drier areas that are less frequented by foraging redshanks, so redshanks may be feeding on them infrequently.

The research confirmed that *Orchestia* were being taken at the study site which supports previous evidence by Cresswell (1994a), Yasue *et al*. (2003), Minderman *et al*. (2006), Cresswell and Whitfield (2008), and Sansom *et al*. (2009). The ribbon-like white threads that were also found may have been a species of cestode tapeworm endoparasite, which are known to exist in the intestines of redshanks (Burt, 1961). The author found heavy infestations, counting 120 of a species he identified as *Ophryocotyle proteus* in one bird. Sánchez *et al*. (2005) also report this endoparasite present in redshanks, but in this case discovered cystoids in faecal pellets. However, no evidence suggests that this endoparasite occurs in the gizzard, and because the threads seemed to occur in pairs which were fused at either end, they may be the remains of *Orchestia* ventral nerve cords which are described by Whitington and Bacon (1997).

3.4.2 Abiotic factors influencing redshank feeding presence

The results showed that in winter redshanks switch their feeding habitat from saltmarsh creeks and the estuary to forage in specific areas of saltmarsh vegetation. This is despite the increased risk of being killed by raptors, particularly sparrowhawks. Reasons for this might be due to lower temperatures, which require them to feed on energetically rich *Orchestia* to satisfy their budget deficit (Cresswell, 1994a; Yasue *et al*., 2003). In addition, their primary prey (*Corophium*) becoming less available (Meadows and Ruagh, 1961; Goss-Custard, 1967; Evans, 1979). They may also need to find shelter on the saltmarsh from stormy weather (Mitchell *et al*., 2000; Yasue *et al*., 2003).

Optimising energetic needs

Metabolic rates and thermoregulatory costs in waders increase along with heat loss, caused by weather conditions such as rain, low temperatures and high winds, which increases their energetic requirement (Wiersma and Piersma, 1994). Yasue *et al*. (2003) discovered that at the study site, redshanks can satisfy these increased energy demands by feeding on the saltmarsh, on larger prey like *Orchestia*, as compared to *Corophium* in the mud, where energetic intake was 23% lower and thermoregulatory costs 40% higher than when feeding in saltmarsh vegetation. This results in them being more vulnerable to predation, but it appears that they are focussing on the immediate threat of starvation (Yasue *et al*., 2003). Nevertheless, this study showed that neither lower air temperature nor increased wind speed were predictors of increased probability of redshanks feeding on the saltmarsh, so these adverse weather characteristics appear not to be the driver behind redshanks changing habitat. It may be that they can make up the energetic deficit by feeding at a greater intensity on *Corophium*, but this was discounted by Goss-Custard (1969) who discovered that there was no increase in intake to compensate for shorter days in winter, nor did redshanks select larger individuals. More recent research by Yasue *et al*. (2003) also indicated that there was no increase in feeding intensity at the study site in mid-winter. During this research, it was discovered that whilst walking up saltmarsh creek mud, as many as 25 redshanks could be seen feeding on *Corophium*. What is possible therefore, is that redshanks extend their feeding time in creeks and on the estuary, and hence make up the intake deficit by feeding at night on *Corophium* and other mud invertebrates such as polychaete worms without needing to put themselves at greater risk by foraging on the saltmarsh. In mid-winter, on the Ythan estuary, northeast Scotland, it was estimated that redshanks managed to obtain less than 50% of their necessary daily food requirement in daylight, feeding on *Corophium, Nereis*, *Macoma*, and so had to supplement their intake by continuing to feed on the estuary in darkness, or in adjacent fields at high water for terrestrial prey (Goss-Custard, 1969). In addition, it was found that in winter redshanks would continue to feed until midnight whereas in autumn and spring they would stop feeding at dusk (Goss-Custard, 1969). However, prey at night and in winter may be harder to find, abundance may be decreased, and therefore, feeding is less profitable (Goss-Custard, 1980; Sitters, 2000).

The effect of wind

Because high wind speed is detrimental to survival in birds (Evans, 1976) they will find shelter to reduce its effect (Lima and Dill, 1990; Mitchell *et al*., 2000; Yasue *et al*., 2003). However, at the study site Hilton, Ruxton and Cresswell (1999) suggested that increased wind speed may mask sound and visually disrupt awareness of the

approach of a sparrowhawk attack, and redshanks responded to this by reducing their foraging on the saltmarsh, and foraged further from cover. One redshank strategy that might provide shelter for birds is foraging in creeks. This was observed where there could be as many as 20 birds feeding in creeks at any one time, usually in the main channel, and in preference to the estuary and on saltmarsh vegetation. Also, redshanks feeding in creeks and hidden from view, were not categorised as present in the study, because they were not feeding on *Orchestia*. Redshanks in creeks might also be less visible to sparrowhawk launch sites, particularly if they are walking underneath creek banks where they are both obscured from view and protected from wind, and especially in creeks (*e.g.* main channel) which run parallel with Little Binning Wood to the west; a regular sparrowhawk habitat. Sparrowhawks perch hidden in the top third of trees and bushes (Newton, 1986), so one would expect redshanks to be in view only part of the time, and although perching higher up may provide an uninterrupted view, sparrowhawks themselves may be exposed to higher wind speeds, which might handicap attacks. In addition, sparrowhawks have been seen to mount attacks by flying up the main creek, which could suggest that their view of redshanks is obscured when perched in trees, and contour-hugging fast, low flight up the creek bed may be a more successful form of attack (Owen, 1932; Pound, 1936). Work at the study site by Sansom *et al*. (2009) in winters 2005/6 and 2006/7 discovered that only 15% of sparrowhawk attacks were mounted against redshanks feeding in creeks, despite creeks being the preferred foraging habitat. However, only 2% of these were by sparrowhawks flying directly up a creek channel (Email, A. Sansom, personal communication, 3 March 2017).

The effect of temperature

Air temperature showed no significant effect on redshank presence. Therefore, despite increased thermoregulatory costs at lower air temperatures, redshanks must still gain their energetic requirement without feeding on *Orchestia*. It is at lower soil temperatures that the probability of redshank presence on the saltmarsh increases. The assumption here is that lower soil temperature equates to lower mud temperature. Although the buffering effect of high tides may raise the temperature of colder mud to that of the surrounding sea[2], during lower high tides and especially at night, areas of mud in creeks may not be covered by seawater, or coverage may be limited for several days. It was observed that mud in creeks freezes at low tide and after hard frosts. During these periods, invertebrates and *Corophium* especially avoid low temperatures (Meadows and Ruagh, 1981) by reducing their surface activity. Surface activity usually involves males emerging from burrows and pulling themselves across the mud surface (Fish and Mills, 1979), and flexing the second antenna outside the burrow entrance (Goss-custard, 1967), which act as visual cues to feeding redshanks (Goss-Custard, 1976; Pienkowski, 1983). The critical mud temperature when *Corophium* become inactive and less available has been reported as 6°C (Goss-Custard, 1970a) and 4°C (Cramp and Simmons, 1983). Goss-Custard (1977c) discovered that alternative prey such as *Nereis* and *Macoma* are not as affected by cold mud temperatures and are still available, so they appeared more in the redshank diet in these conditions; however, *Nereis* were found to provide a poorer energy return than *Corophium* and both species might be locally scarce (Goss-Custard, 1977c). At the study site random sampling in creek mud only found occasional *Nereis* and *Macoma,* whereas on the estuary they were more common. It would seem therefore, that once *Corophium* become less available due to low temperatures, extended feeding

[2] The sea temperature of coastal waters surrounding Dunbar in February ranges between 5.2 – 7.4°C with a mean of 6.5°C (World Sea Temperature, 2017).

time does not satisfy redshank energy demands and neither does switching to other invertebrate prey in mud. In these situations, redshanks switch feeding to *Orchestia* on the saltmarsh, despite the increased risk of predation.

High tide height and time

Redshank presence on the saltmarsh was more likely around the lower neap tides, possibly because more saltmarsh habitat was available to forage on at high tide. Moreover, *Corophium* possess a rhythm entrained to the spring to neap cycle where swimming activity maxima is reached, at or just following spring tides which have the widest tidal range (Harris and Morgan, 1986). If this is independent of other variables such as wind and temperature, foraging redshanks can probably take advantage of this increased activity by concentrating feeding on *Corophium*, satisfying their energetic needs by foraging in the creeks and estuary and not on the saltmarsh vegetation. In contrast, during neap tides *Corophium* swimming activity is supressed, which may mean that visual cues to redshanks may be reduced resulting in them switching feeding to *Orchestia* in saltmarsh vegetation. However, time of the nearest high tide showed that the probability of redshank occurrence increased between high tide times of 0300 hrs and 1800 hrs, also described in this system by Quinn and Cresswell (2012). This appears contradictory because the highest high tides in winter occur between midday and midnight, and the lowest high tides between midnight and midday. For instance, during the fieldwork period in winter 3, 88% of high tides between 1200 and 1800 hrs were ≥4.9m, but only 12% of high tides <4.9m occurred between the same times. The reason for this may be because redshanks are focusing on the predation risk by congregating in larger flocks in which they feel safer, forced onto smaller areas of saltmarsh not covered by seawater and on the outer edge close to sparrowhawk-concealing cover. Quinn and Cresswell (2012) found that in this case, concerted cumulative attacks by sparrowhawks prompted better quality birds to escape and find less vulnerable areas during the highest high tides, leaving a reduced flock size of poorer quality, more vulnerable birds (*e.g.* juveniles), which were at greater risk.

Seasonal effect

Because day number was entered as a smoothed variable in the GAM where extra quadratic regressions were fitted to maximise the line of best fit in the model (Thomas *et al*., 2015), the results showed a reduction in redshank presence on the saltmarsh from the third week in November until the beginning of January when it began to rise, reaching a peak in the third week in January before decreasing again. The initial reduction only occurred in winter 3 and is probably down to a fluctuation in numbers caused by the onward migration of birds in the autumn, which finished by the end of the year. An influx of more Icelandic birds would start to swell the numbers again by the beginning of January, as described by Prater (1981). It is unlikely that reduction in autumn was caused by starvation mortality as weather conditions were normal for the time of year and there was little evidence of hunting sparrowhawks and no kill remains were found during this time. It is highly likely that predation risk from sparrowhawks has decreased at the study site as mean winter temperatures have increased over the last 25 years (Cresswell and Whitfield, 2008).

3.4.3 Biotic factors influencing redshank feeding presence

Feeding in Orchestia profitable areas

Redshanks did not feed in the most profitable *Orchestia* patches and they were more likely to feed on the outer saltmarsh especially to the west and the north. These were areas mainly inhabited by *O. gammarellus*. Because the majority of redshanks that feed on the saltmarsh are first year juveniles (see 3.1.2, page 80) (Cresswell, 1994a; Cresswell and Whitfield, 1994), it may be that they are less adept at targeting *Orchestia* patches, which are an atypical food resource that might require modification of their normal feeding behaviour. Reduced foraging efficiency amongst juvenile birds has been detailed by Ashmole (1963) for tropical seabirds, Partridge and Green (1985) in theoretical studies, Goss-Custard (1987) for oystercatcher (*Haematopus australegus*), Dukas and Kamil (2001) for blue jay (*Cyanocitta cristata*) and Bijeleveld *et al*. (2012) and van den Hout *et al*., (2014) for red knot.

Vegetation species, structure and feeding technique

Perhaps the most likely reason why redshanks do not feed in the most profitable *Orchestia* areas may be due to the feeding technique they employ in differing vegetation structures of saltmarsh plants, and their inability to simultaneously detect the predation risk. *O. gammarellus* are more likely to be found in grass, especially *F. rubra* on the outer marsh. Twelve of the 11 highest samples of *O. gammarellus*, >10 individuals (mean 13.36 ± 0.88 SE), occurred on the outer boundary of the saltmarsh where vegetation had a mean density of 95% ± 1.2 SE, and consisted mainly of *F. rubra*. These sample points were not associated with the densest redshank feeding areas (Figures 3.3, 3.4). However, feeding occurred very close to the boundary edge in other vegetation communities, mostly stanchions of the short, patchy *A. maritima* and *F. rubra*/*A. maritima* mixed habitat. It is suggested that although the technique of probing thick grass like *F. rubra* may be profitable, it puts redshanks at greater predation risk, because not only are they closer to predator-concealing cover, but the action of touch-probing with head down compromises their ability to detect predators. In contrast, when they forage in *A. maritima* and the *F. rubra*/*A. maritima* interface, their technique is different; they feed visually by pecking at prospective food items, and most of the time their head is up, which allows them to scan for threats; the drawback is that this habitat is less productive. Nevertheless, it may allow them to feed close to the boundary, especially if flock sizes are larger and there are more individuals to spot an attack.

Saltmarsh creek edges are also places targeted by foraging redshanks (Yasue *et al*., 2003). They are often fringed by grasses *F. rubra* and *P. maritima* and are areas of higher *Orchestia* density. The adjacency of *P. maritima* to creek edges mainly in the mid saltmarsh region may be why the best model showed a positive association to feeding areas compared to non-feeding areas, although this was contradicted by preliminary NMDS scaling diagrams for both winters 2 and 3 where it was more associated with the latter. Creeks are most common in the north central marsh and slightly to the west, where a network of small creeks drain into the main channel. This is mainly *O. gammarellus* habitat, and was another redshank priority feeding area especially in winter 3 (Figure 3.1). Two methods of foraging were observed here. First, birds forage close to the edge of the creek where they can detect prey visually on *A. maritima*, and probe for prey in *F. rubra* on the creek edge. Probing is less hazardous here because the area is further from the saltmarsh boundary. Second, redshanks walk in the small creeks and are

mostly hidden from view and feed on *Corophium*, but they were also observed feeding on *Orchestia* from the creek bed by pecking the top of the creek bank. *Orchestia* try to escape by crawling or jumping but often they land in creek mud where they can be picked up. This feeding technique may act as a stimulus for redshanks to move out of the creek and onto the creek edge to take advantage of higher *Orchestia* densities.

Redshanks were only occasionally found foraging on the mid and inner saltmarsh where *O. mediterranea* is the most prevalent species. The inner saltmarsh species *S. europaea* showed a marginally non-significant negative effect as occurring in redshank feeding areas, probably because the open single stem plants on the edges of the estuary do not offer protection for *Orchestia* which are rarely present. Although increased numbers of *Orchestia* tend to be correlated with greater overall vegetation density, feeding redshanks were not associated with these areas. The reason is probably that redshank feeding areas are a mixture of dense grass such as *F. rubra* (and occasional *P. maritima*), and more open *A. maritima*, so areas are not homogeneous in their density, but made up of an alternate patchwork of dense and sparse areas. Therefore, quadrat sampling was unable to differentiate this variation; a quadrat might be randomly placed on a *F. rubra* patch with full cover, or alternatively an *A. maritima* patch close by that was mainly bare soil with very few plants. Feeding redshanks were however more likely to occur in shorter vegetation, which included *A. maritima* and *F. rubra,* the latter which grows outwards rather than upwards. Redshanks tend to avoid feeding in taller vegetation especially *A. tripolium* which occurs on the mid and inner marsh, even though this plant is associated with *O. mediterranea* presence. This might be for two reasons. First, taller vegetation may impede redshank feeding technique and interfere with their focus, also mentioned by Butler and Gillings (2004) for lapwings, Whittingham and Evans (2004) for starlings, and Furnell and Hull (2014) for waders in general. Second, taller vegetation may obscure detection of the flight approach of sparrowhawks and provide an obstruction to escape, which has been reported in chaffinches (Butler *et al.*, 2005).

3.4.4 Conclusion

Optimal foraging and how species modify their behaviour to collect food with the least amount of energy expended, and at the lowest predation risk, is paramount to survival. In this system, the aim for redshanks is to manage the two main threats of starving to death or being killed by sparrowhawks. The research so far has found that wind may be an important factor in redshanks choosing the shelter of creeks as their preferred foraging habitat. Creek-foraging has the added benefit of giving some protection from sparrowhawk attack and enabling redshanks to feed on their preferred prey, *Corophium*. In this situation starvation-predation risk is low and redshanks can optimise their energetic requirement, shielded from the wind, at a safe distance from trees that bound the saltmarsh that may conceal sparrowhawks, being partly sheltered from view. It is only when soil temperature and more importantly mud temperature falls and *Corophium* become less available, that redshanks need to assess the immediate concern of finding food so they modify their feeding behaviour, by relocating to the saltmarsh. Not only is this habitat less sheltered than creeks, but their new prey source, *Orchestia*, occur in areas that are at greater predation risk for redshanks, which requires them to reappraise the starvation-predation risk priority. Feeding position, head down probing or head up pecking, is dependent on vegetation type and density, and may influence their awareness to the predation threat. They are prevented from feeding in safer areas on *O. mediterranea* because vegetation height may restrict feeding technique, the detection of predators, and possibly impedes their escape. Lower temperatures also reduce the activity of *Orchestia* which may make them more cryptic and harder to detect.

Therefore, the bottom-up process is not just a linear connectivity of species and energy flow, but a much more complex series of interactions controlled by abiotic and biotic influences that affect both predator and/or prey. In addition, it appears that bottom-up processes may work in tandem with top-down. The next chapter will investigate redshank flock size and whether larger flocks are able to better exploit *Orchestia*-rich areas, and how weather and especially temperature influences redshank foraging. It will also further explore how redshanks alter their feeding behaviour in different vegetation types.

CHAPTER 4. PREDICTING REDSHANK FLOCK SIZE AND FEEDING BEHAVIOUR

4.1 Introduction

An animal's behavioural response to the threat of predation is fundamental to our understanding of relationships between trophic levels and how ecosystems are structured (Lima, 1998a; Agrawal, 2001; Werner and Peacor, 2003; Abrams, 2010). Animals need to modify their feeding behaviour to assess whether predation or starvation is the greatest immediate threat. This starvation-predation risk trade-off largely determines a species' distribution and whether it preys on animals at a lower trophic level, competes with individuals at the same trophic level, or is prey for animals at a higher trophic level (Cresswell, 2008). Therefore, in this system redshanks predate *Orchestia*, whilst being in competition with conspecifics and other wader species, but are themselves preyed upon by sparrowhawks (Yasue *et al*., 2003; Minderman *et al*., 2006). The size of a group is also important in mitigating vulnerability to predation (Krause and Ruxton, 2002; Caro, 2005) and so has a bearing upon both predator and prey (Abrams, 1993). For redshanks this can mean safety in numbers, where there is more chance of at least one bird detecting a predator and raising the alarm, less chance of being the subject of an attack, and more escaping birds causing confusion for the attacker (Cresswell, 1994b; Hilton, Cresswell and Ruxton, 1999; Lind and Cresswell, 2005; Quinn and Cresswell, 2005). The techniques that redshanks use to feed may also have a bearing on how they balance this starvation-predation risk trade-off. An example at the study site is provided by Sansom *et al*. (2009) who determined that a redshank feeding with its head up was more vigilant than if it fed with its head down, but this might impact upon its feeding rate and success. Variability in flock size and feeding behaviour due to difference in a variable such as temperature thus provides an indication of whether that variable is important in the starvation-predation risk trade-off and trophic dynamics. In short, although animal species such as redshanks will aim to take advantage of the best feeding areas, they simultaneously have to evaluate predation risk (Carey, 1985; Lima *et al*., 1987). The question is, why redshanks favour specific areas: how much do abiotic variables and type of vegetation habitat control redshank flock size and feeding directly, or indirectly by influencing *Orchestia* behaviour which then affects redshanks. This should determine how redshanks make-up energetic shortfall by feeding on *Orchestia*, thus easing the starvation risk, but which may at the same time put them at a greater risk of predation.

The first part of this chapter will look at redshank feeding flock size and investigate what influences it. Although abiotic confounding effects of year, high tide height, time of the nearest high tide, and seasonal effect will be considered in models, other predictors of flock size such as temperature, wind speed, distance to the saltmarsh boundary, type of vegetation and *O. gammarellus* density should also give an indication as to what controls numbers of redshanks feeding on the saltmarsh. In the second part of the chapter redshank feeding behaviour will be investigated which will include their walking effort, feeding effort and feeding success, against relative abiotic and biotic variables. This should allow a better understanding of how redshanks manage the trade-off between predation and starvation risk and what influence *Orchestia* have on this. Nevertheless, results in Chapter 3 show that the most profitable *Orchestia* patches do not necessarily correlate with the presence of feeding redshanks, suggesting that other components, such as the perceived predation threat and behaviour of *Orchestia* must influence redshank feeding distribution and behavioural activity.

4.1.1 Group size

There are many examples of species forming larger groups as an anti-predation strategy. The rate of capture by predatory wasps of the web-building spider *Metepeira incrassata* reduces as spider colony size increases (Uetz *et al*., 2002); smooth-billed anis (*Crotophaga ani*) catch fewer butterflies when they are in larger swarms (Burger and Gochfeld, 2001); and the predation rate of lone white-nosed coatis (*Nasua narica*) by jaguar (*P. onca*), is higher than when they are in groups (Hass and Valenzuela, 2002). In birds, larger flocks of woodpigeons were shown to be less vulnerable to successful attack by goshawks (*A. gentilis*) (Kenward, 1978), whilst dunlins (Barbosa, 1997) and other wader species (Goss-Custard, 1970b) increase flock size when under higher predation risk.

A larger group might be more vigilant, have a reduced probability of capture for an individual (dilution effect), provide better defence, and attract conspecifics to profitable feeding areas (Krause and Ruxton, 2002). Moreover, more escaping prey might confuse the predator and reduce the probability of capture (confusion effect) (Roberts, 1996; Schradin, 2000; Ioannou *et al.*, 2008). Meta-analysis of fifty species of bird and mammal by Pulliam (1973), reported that there was a negative correlation between group size and vigilance, where the larger the group, the more time individuals could spend feeding, because more pairs of eyes were available to detect predator attack; what Pulliam (1973) terms the benefits of "*collective detection*". The dilution effect has been observed for a marine insect subject to predation by fish, where swarming behaviour resulted in a reduced chance of an individual being killed (Foster and Treherne, 1981). The confusion effect, where fleeing prey manage to disrupt a pursuit, is described by Neill and Cullen (1974), who found that when small prey fish were chased by ambush predators, pike (*Esox lucius*), squid (*Teuthida* sp) and cuttlefish (*Sepiida* sp), larger shoals produced hesitation and uncertainty in the pursuer. For a chasing predator such as perch (*Perca fluviatilis*), large shoals forced it to switch targets making the pursuit less effective (Neill and Cullen, 1974). These behaviours produce an exponential decline to an asymptote for predation risk as groups become larger (Pulliam, 1973; Elgar and Catterall, 1981; Roberts, 1996). Research into redshanks at the study site has found that larger flock sizes benefit from the dilution and confusion effects (Cresswell and Whitfield, 2008), increased vigilance and the dilution effect (Whitfield, 2003; Cresswell and Quinn, 2004; Quinn and Cresswell, 2004), and vigilance, confusion and dilution effects (Cresswell, 1994b; Hilton, Cresswell and Ruxton, 1999; Lind and Cresswell, 2005; Quinn and Cresswell, 2005). Nevertheless, Sansom *et al*. (2009) found that greater vigilance when foraging in larger flocks was cancelled-out by interference competition. In addition, Cresswell and Quinn (2011) discovered that a group size threshold exists above which the alleviation of predation risk is negligible and disadvantages to grouping become apparent, so there is little profit in forming larger groups above this threshold. Hence, the dilution effect leading to a reduction in attack rate was advantageous only up to a certain flock size, although attack rate success continued to decline as the size of flock increased (Cresswell and Quinn, 2011).

Although increased group size is advantageous, there might also be costs (Lind and Cresswell, 2005), which may include food competition, kleptoparasitism, interference competition and being more conspicuous to predators (Krause and Ruxton, 2002). Vine (1973) stated that larger prey groups might be more visible to a predator and therefore are at a disadvantage. In addition, it has been found that cichlids and wolf-fish (*Hoplias malabaricus*) attacked shoals of guppies (*Poecillia reticulate*) in preference to a single guppy and attacked on more occasions;

attack and success rate by sparrowhawks increased on flocks of finches (*Fringilla* sp) in the autumn when these were larger (Lindstrom, 1989); predation by peregrines was increased on larger starling roosts (Carere *et al*., 2009); and larger redshanks flocks were more likely to be attacked by sparrowhawks, but contrastingly these attacks were more likely to succeed if attacking smaller flocks (Cresswell, 1994b).

Temperature is likely to affect the activities of both predator and prey, and thus influence the starvation-predation risk trade-off and so optimal group size. A wader needs to conserve body temperature to maintain its metabolism so that it can continue with normal functions such as digestion, and behaviours like foraging, flying and escaping predators (Evans, 1976). Colder temperatures will increase heat loss from the skin and feathers and require it to increase its intake so as to balance greater energetic expenditure (Evans, 1976); although Davidson and Evans (1982) stated that at very low temperatures waders generally are able to draw on fat reserves to replace this shortfall, death usually occurs after these reserves have been exhausted. The problem they face is that the most energetically rich areas tend to have a greater predation risk (Houston *et al*.,1993), although larger flocks and the associated benefits of increased collective detection, and dilution and confusion effects may allow prey to mitigate the risk and feed in these areas (Pulliam, 1973; Cresswell, 1994b; Hilton, Cresswell and Ruxton, 1999; Lind and Cresswell, 2005; Quinn and Cresswell, 2005). Previous research has indicated that at higher temperatures, surface activity of invertebrate prey increases. Pienkowski (1983) found that when it was warmer polychaetes *A. marina* and *Notomastus latericius*, amphipod *Bathyporeia pelagica*, and isopod *Eurydice pulchra* became more active; Evans (1979) stated that *C. volutator* crawl on the surface of the mud and protrude out of their burrows; and earlier initiation of movement by males and breeding activity of *O. gammarellus* takes place (Morritt and Stevenson, 1993). As has been discussed in Chapter 2, at higher temperatures *Orchestia* move quicker and crawl and jump more, and therefore may become more available, attractive to redshanks and so increase redshank flock size. A contrasting effect is caused by low temperatures, where several invertebrate prey species burrow deeper and movement reduces including: *A. marina* (Smith, 1975), *N. diversicolor* (Evans, 1979), *Macoma balthica* (Reading and McGrorty, 1978), and *C. volutator* (Goss-custard 1967, 1969 , 1976, 1977c). On cold days, *Orchestia* curl up, are unresponsive and their movements are slow (pers. obs.). Lower temperatures may thus make invertebrate prey less conspicuous (they become more cryptic) and reduce their availability because they retreat into refuges and this reduces their availability for waders, decreasing flock size. Hence, temperature can affect the starvation-predation risk trade-off by influencing the size of the group and causing behavioural change at more than one trophic level.

Previous research has given mixed results for the effects of temperature on flock size and the starvation-predation risk trade-off. Although findings so far indicate that air temperature has no significant effect on the increased probability of feeding redshanks being present on the saltmarsh, one piece of research at the study site has described a link between increased flock size and lower air temperatures (Hilton, Ruxton and Cresswell, 1999), whilst another found no significant effect (Cresswell *et al*., 2010). However, Cresswell and Whitfield (2008) discovered that cold air temperatures had a profound effect, where to optimise their intake by feeding on energy-rich *Orchestia*, redshank numbers on the saltmarsh increased. Sparrowhawks can take advantage of this so that at low air temperatures, redshank capture rate was increased (Hilton, Ruxton and Cresswell, 1999). When Yasue *et al*. (2003) looked at air temperature, they suggested that the greatest mortality in redshanks was not caused by

starvation, but by the indirect relationship between cold air temperatures that increased starvation risk, which forced them to relocate onto the riskier saltmarsh habitat, resulting in an greater predation risk. The effect of soil temperature on redshank flock size and feeding behaviour has previously received little attention. It has been shown that soil temperature corresponds to, but lags behind air temperature change (Toy *et al*., 1978), but as results have so far shown, it is soil rather than air temperature that influences redshank presence on the saltmarsh. It is therefore expected that a drop in soil (mud) temperature is an important driver in increasing the size of feeding flocks that are forced to switch feeding from mud-dwelling *Corophium* which become less active and burrow deeper, to *Orchestia* on the saltmarsh. In addition, perhaps redshanks can feed more productively when low soil temperatures reduce *Orchestia* movement and slows reactions.

Wind speed is also likely to affect the activities of both predator and prey, and thus influence the starvation-predation risk trade-off and optimal group size. For birds, the increase in metabolic rate (Gessaman, 1973) and energetic costs (Masman *et al.*, 1986; van Mannen, 2001) leading to increased starvation risk, and difficulties faced in foraging (Dugan *et al*., 1981), are all limitations caused by increased wind speed. In a study undertaken in northeast Scotland, shelter from wind and food quality and quantity were the primary concerns of red deer (*Cervus elaphus*), which preferred lee slopes and congregated in herds in dips and behind heather (Staines, 1976, 1977). Similarly, when groups Scottish mountain hares (*L. timidus scoticus*) shelter behind peat banks in heather, or in snow scrapes, they reduce the effects of wind by 84-90% (Thirgood and Hewson, 1987). Johnston (1942) found that in winter and early spring, 12 species of woodland bird moved to the lee side of woods in a strong prevailing wind, and changed position in the wood dependent on the wind direction. It has also been suggested that for roosting flocks of Phainopepla (*Phainopepla nitens*), a small desert songbird, it is shelter from wind and not necessarily low temperatures, that allows the bird to reduce radiation loss (Walsberg 1986). Dolby and Grubb Jr (1999) in research in Ohio discovered that four species of bark-foraging woodland birds were found furthest away from wind-exposed edges of small isolated copses when wind speed was high and temperatures were low (<-6°C). Even though Yasue *et al*. (2003) indicated that wind speed is responsible for higher numbers of redshanks relocating to the saltmarsh, results from Chapter 3 during the course of this study indicate that higher wind speeds had no significant effect on the likelihood of redshanks being present. Nevertheless, presence and abundance are different measures, so it might be that redshank flocks grow larger as wind speed increases with more birds escaping to the more sheltered habitat.

Distance to predator-concealing cover may influence flock size and the starvation-predation risk trade-off, where decisions need to be made on the time spent in low risk and high risk habitats, and thus the time dedicated to foraging and vigilance behaviour respectively (Inger *et al.*, 2006; Watson *et al*., 2007). Yellow-bellied marmots prefer to forage away from vegetation that might conceal predators (Carey, 1985), and several species of African antelope avoid cover as they perceive it as a risky habitat where predators may be obscured from view (Underwood, 1982). Lima *et al*. (1987) found that three species of finch (Emberizidae) fed well away from cover although the benefit from increased energy intake was negligible. The authors went on to suggest that they viewed feeding close to cover and at distance, to be equally risky and that the birds applied a trade-off to assess the greatest threat. In contrast, Schneider (1984) found that white-throated sparrows, fed closer to cover until food was exhausted, before then moving further away, which suggested that they viewed foraging in open areas as a

risk. Other research by Ekman (1987) on willow tits (*Poecile montanus*) indicated that subordinate birds were forced to feed in exposed patches that required them to be more vigilant, which reduced their energetic intake. Previous research at the study site suggests that redshanks maximise their distance from cover when the starvation threat is low and there is no requirement to forage in profitable but risky patches on the outer saltmarsh close to trees (Cresswell *et al*., 2010). Cresswell (1994a), suggested that redshanks feeding on the saltmarsh less than 50m from cover, were at greater risk of predation compared to those feeding on *Corophium* in the estuary, where birds were often widely spaced and could be up to 200m away from predator-concealing trees and shrubs. Distance between sparrowhawk attack position and the target is critical to the redshank's escape strategy, and where these distances are short, any delay in taking flight can result in a much greater probability of capture (Hilton, Cresswell, Ruxton, 1999). Whitfield (2003) found that increased distance from cover and flock size when employed together, were both advantageous to redshanks, though the latter to a lesser extent. He went on to say that this behaviour had little effect on sparrowhawk success rates which remained constant, but Cresswell and Quinn (2004) suggested that the probability of hunting success increased when birds were in smaller flocks and closer to cover. Feeding patches further from cover may be less profitable, which can result in interference competition amongst larger flocks, which then increases starvation risk and so redshanks are forced to feed closer to cover in widely spaced groups to reduce interference competition, but where they are more vulnerable to attack (Minderman *et al*., 2006; Cresswell and Whitfield, 2008).

All the variables described above may be modified or interact with vegetation, which could impact upon the availability of prey and the ability to detect and avoid predators, and so vegetation may fundamentally affect flock size and the starvation-predation risk trade-off. For example, birds foraging in winter in a particular habitat may be more reliant on certain species of vegetation than birds that occupy the same habitat in summer. This could be because invertebrate prey shelter in specific plants and communities, and are less abundant and available at this time of year (Anderson *et al*., 1983). An example of this is given by Meents *et al*. (1982) in research in a riparian habitat in Colorado where sage sparrows (*Prosopis glandulosa*) are predominant in honey mesquite habitat, but in winter, inkweed (*Suaeda torryana*) was preferentially selected for foraging and held greater densities of sparrows (Meents *et al*., 1982). Robinson and Holmes (1984) also describe similar results for four woodland bird species in New Hampshire, which exploit specific understory plants that contain the highest number of arthropods. Results from Chapter 3 have shown that redshanks are more likely to feed in patches of *F. rubra*, *A. maritima* and *A. maritima*/*F. rubra* mixed habitat on the outer saltmarsh and on the edge of creeks where the probability of finding *O. gammarellus* is greater. To a lesser extent, they are also more likely to be found feeding in *P. maritima* which displaces *F. rubra* in some areas towards the mid-marsh, although this species of vegetation is not associated with an increased probability of *Orchestia* occurrence or abundance. Flock size may then increase along with the density of individual vegetation species. However, because the range in the density of some species is quite narrow; for instance, 74% of plots where *F. rubra* is present range between 50% – 85% density (mean 64% SE ± 3.4, *n* plots = 126), and 64% of *A. maritima* plots, 1% - 48% density (mean 34% SE ± 1.7, *n* plots = 189), it is unclear if an association between flock size and vegetation density will be found.

Prey behaviour may also influence flock size and the starvation-predation risk trade-off. Predators are expected to concentrate feeding effort in the most profitable areas, where profitability relates to increased energetic or

nutritional benefits (Royama, 1971). Goss-Custard (1977b) further defined profitability as ingestion rate and found that this was greatest when redshanks fed in the densest *Corophium* patches, where they also foraged for longer. At the study site, we have seen that redshanks are most likely to be present as *O. gammarellus* density increases, but unlike *Corophium* as described by Goss-Custard (1977b), this likelihood decreases at the highest *O. gammarellus* densities. But as more animals congregate where food is densest, so they will start to compete for this food because as the group becomes larger, the resource is overexploited (Milne, 1961). Goss-Custard (1980) termed this interference competition, so that an increase in predator density results in a reduction in intake rate. This produces a more immediate effect than depletion of prey, although both are reversible but replenishment of prey may occur over a longer timescale (Goss-Custard, 1980). Intake rate may also be reduced due to depression of the resource which was described by Goss-Custard (1976) for *Corophium* which withdrew into their burrows following increased surface activity by redshanks. Minderman *et al*. (2006) described prey depression by redshanks on *Orchestia* at the study site and went on to say that a reduction of intake rate was unlikely to be the result of depletion. It is expected that flock size will also increase with an increase in *O. gammarellus* density, to a level where interference competition reduces foraging success and prey depression occurs. Redshanks then become more spaced and at greater risk of predation, which results in them relocating to undisturbed feeding areas.

High tides may also have an effect on flock size. Evans (1976) indicated that waders have greater difficulty feeding in mid-winter when the ground extent was reduced by high tides, and food intake was least when high tides occurred around midday. For high tides above 4.5m none of the estuarine mud is available to feeding redshanks, and as tides get higher (days around the highest high tides), even less of the saltmarsh is available for feeding (pers. obs.). This was also noted generally by (Prater, 1981) for wader species, and at the study site by Cresswell and Whitfield (2008) and Sansom *et al*. (2009) who suggested that in these conditions flocks would be larger. However, in Chapter 4 we found that redshanks were more likely to feed on the saltmarsh on days when there was a low high tide, and contrastingly, when there was a high high tide in the afternoon. It is expected that flock size will also increase in line with these results. However, attacks on waders by sparrowhawks at high tide were found to be more frequent by Whitfield (1985, 1988) and higher attack rates lead to smaller flock sizes on the study site (Quinn and Cresswell, 2012). Nevertheless, although they will be recognised as having an influence on flock size, high tide height and time of the nearest high tide will be largely considered only as confounding variables.

Finally, there may well be confounding seasonal effects to consider on flock size and the starvation-predation risk trade-off. Prater (1981) mentions that it is not until December/January that redshank numbers reach their winter peak in Britain, with fewer birds post migration in the autumn (due to increased mortality) and in early spring after the onset of return migration. *Orchestia* behaviour may be responsible for an opposite effect, because male *Orchestia* activity has been recorded as increasing in early spring, where they go in search of females prior to breeding (Moore and Francis, 1986b). More active *Orchestia* later in the season may provide a visual cue that provokes redshanks to switch feeding to the saltmarsh, resulting in larger flocks forming.

4.1.2 Feeding behaviour

Feeding behaviour is affected by the starvation-predation risk trade-off, where an animal's feeding strategy responds to environmental influences, so that it can maximise calorific intake, minimise search effort, whilst simultaneously watching for predators (Pulliam, 1974), and this can impact on flock size. Feeding strategy for a redshank might include pecking at surface prey or reacting to visual cues of that prey (Goss-custard, 1967, 1976, 1977c; Dias *et al*., 2009), and probing hidden prey where it feeds by touch (Goss-Custard, 1976; Dias *et al*., 2009). Other behaviour such as number of steps may give an indication of feeding intensity and success (Dias *et al*., 2009; Santos *et al*., 2009), and it has been suggested that redshanks that have a higher step rate when feeding on *Orchestia*, have reduced success, greater spacing and this results in an increased predation risk (Minderman *et al*., 2006). In addition, interference competition may be greater where birds detect their prey by pecking, rather than probing (Goss-Custard, 1976). As previously explained, there may also be a conflict between feeding methods and levels of vigilance so that when a redshank is probing with its head down, awareness of the predation threat may be reduced (Sansom *et al*., 2009). Variables such as *Orchestia* density, temperature, season, tidal influence, distance from the saltmarsh boundary and distance from the nearest creek edge, may therefore dictate what type of feeding behaviour a redshank employs.

As generalist foragers, redshanks employ a variety of different techniques specific to other waders when feeding. They can turn over gastropods and scavenge half-emptied bivalve shells, probe for prey in the subsoil, peck on the surface at moving prey, and hunt by stealth (Goss-Custard, 1975). The majority of previous research describes them foraging for *C. volutator*, polychaete worms (Goss-Custard, 1977c), *Hydrobia* and the bivalve *M. balthica* (Goss-Custard, 1969). Of these, Goss-Custard (1977a), discovered that their preferred prey is *C. volutator* followed by *Nereis*, and even when both are abundant, stimuli produced by *Corophium* make them easier to detect, so they then become the major focus of their feeding effort. Redshanks are to be found feeding mostly on estuarine mud, which they peck with rapid short movements (Goss-Custard, 1966), and only occasionally by touch (Goss-Custard, 1977a). Dias *et al*. (2009) indicated that redshanks forage on the surface mainly by using visual cues, but can switch to subsurface touch-feeding (probing), if this becomes more profitable. Foraging by touch may be the only means of foraging at night where redshanks have to augment a deficit in their energetic intake (Goss-Custard, 1969), although Evans (1976) suggests waders feeding by touch will only be effective at high prey densities and where prey is uniformly spaced. Sutherland *et al*. (2000) investigated foraging in western sandpipers (*C. mauri*) comparing two feeding methods; picking copepods and cumaceans off the epibenthos, and probing for infauna such as polychaete worms. They found that when prey had retreated below the surface, they used tracks or worm casts as visual cues to locate prey before employing a tactile probing technique using the bill to test for vibrations, taste (via chemoreceptors in the tip of the bill), and to sense differences in pressure gradients in mud/soil interstitial water (Sutherland *et al*., 2000). Gerritsen and Meiboom (1986) found similar feeding behaviour in sanderlings (*C. alba*), and Pienkowski (1983), suggested that ringed (*C. hiaticula*) and grey plovers also use surface visual cues including casts from *A. marina* and water spurts from polychaete holes, before probing just below the surface. It may be that the redshank bill has similar morphological characteristics to those of other waders which enables it to switch between feeding visually by surface pecking, to probing for subsurface prey.

Prey depression may occur if redshanks feeding visually on the surface disturb prey by walking. Prey may then

retreat into burrows in the mud as with *Corophium*, or into the subsoil as with *Orchestia*. However, it is suggested that if they reduce their step rate this lessens the effect, which also gives them more time to scan for prey (Goss-Custard 1977a; Gendron and Staddon, 1983). Interference competition can reduce success rate because redshanks hunting surface prey by sight are distracted by conspecifics, whereas when feeding for prey below the surface using touch, birds can feed closer together, feed more slowly and extend residence time in an area (Goss-Custard, 1976; Goss-Custard, 1980; Sutherland *et al*., 2000). Similarly, interference competition may impact on *Corophium* availability if intense grazing of surface prey outstrips replenishment from subsurface burrows, leading to a reduction in both consumable prey and redshank feeding rate (Goss-Custard, 1970b).

Redshank body position when feeding may also impact upon the starvation-predation risk trade-off, where higher vigilance results in an increased probability of detection of a predator, successful flight escape and hence a better chance of survival (Hilton, Cresswell and Ruxton, 1999; Quinn and Cresswell, 2005), but at the expense of less attention paid to foraging. Blue tits (*C. caeruleus*) were investigated by Kaby and Lind (2003), to determine if body posture, either head up or head down, interfered with their ability to detect raptor attack. This had no effect, but time taken to process whole mealworms resulted in detection being delayed by 150% compared to chopped mealworms. Therefore, the position of the head did not decrease vigilance as such; this was caused by an increase in food processing time (Kaby and Lind, 2003). Nevertheless, research by Sansom, *et al*. (2009) indicated that redshanks were only vigilant when they had their heads-up, rather than at the horizontal or below. Therefore, if greater attention is being paid to probing denser vegetation (*e.g. F. rubra*) for *Orchestia* with their heads-down, this might impact upon predator detection and speed of escape. Pecks at the surface may not affect vigilance because birds are less intent on feeding and head down time is reduced. In addition, Cresswell *et al.* (2003) found that chaffinches that had higher intake success could spend more time being vigilant and reduce predation risk, which might mean that the best foragers are also more adept at detecting predators.

As discussed above, in the context of redshanks avoiding predator concealing cover, the availability of their *Orchestia* prey and how this interacts with vegetation and temperature which may make prey more detectable or able to escape, will be an important factor in determining redshank feeding behaviour and the starvation-predation risk trade-off. We have seen that *Orchestia* activity is dependent upon temperature, therefore, their movement cues may decide the most effective redshank feeding strategy, and probing may be more successful in cold temperatures when *Orchestia* are less mobile and thus more cryptic. In contrast, at higher temperatures a better technique for foraging redshanks may be to peck at moving *Orchestia* on the surface. Because *Orchestia* movement may be influenced by time of year, where they become more active in early spring prior to breeding (Moore and Francis, 1986b), pecking rather than probing at this time may be the preferred feeding technique.

One final factor may also influence redshank feeding behaviour at the study site. Cresswell and Whitfield (1994) suggested that that redshanks were more vulnerable to sparrowhawk attack the closer they were to creeks, although Hilton, Ruxton and Cresswell (1999) and more recently Cresswell and Quinn (2011), maintained that creeks are a safer habitat. Results from Chapter 2 indicate that both species of *Orchestia* were more likely to be present and more abundant, close to creek edges, so redshanks feeding intensively by probing with head down, may be more prone to being killed by sparrowhawks. Probing is more likely to be the favoured feeding technique at creek

edges because this is where dense swards of *F. rubra* occur and the visual detection of prey is reduced.

4.1.3 Objectives

This chapter will investigate firstly what influences redshank flock size and how this relates to the starvation-predation risk trade off in terms of abiotic and biotic predictors.

21. Weather (air temperature, soil temperature and wind speed). The prediction is that as temperatures become colder and wind speed increases, so will flock size, because a redshank's energetic requirement cannot be satisfied by simply feeding on mud invertebrates (*e.g. Corophium*), which may also become less available to redshanks. However, although increased flock size may reduce the risks of sparrowhawk attack, this might cause interference competition that reduces intake success.

22. Distance to the saltmarsh boundary (predator concealing cover). Because, redshanks feel safer in larger flocks, it is predicted that when larger flocks form, they can feed closer to the saltmarsh boundary (sparrowhawk-concealing cover), which will enable them to exploit denser patches of *Orchestia* previously unavailable to them.

23. Vegetation habitat. It is hypothesised that redshank flock size will be larger when birds forage in vegetation such as *F. rubra*, which is more likely to hold *O. gammarellus*, *A. maritima* where results in chapter 3 suggest that redshanks are more likely to be found, and the interface between these two species of vegetation.

24. *O. gammarellus* density. Results so far have shown that an increase in redshank feeding presence was associated with an increase of *O. gammarellus* density, before a decline at the highest densities. Therefore, it is hypothesised that flock size will follow a similar pattern.

25. Confounding effects of tide. It is predicted that when tides are at their highest during spring tides, flock size will increase because there is a reduction of uncovered areas to forage. Similarly, as time to the nearest high tide decreases flock size should increase as birds are forced onto uncovered areas of the saltmarsh.

26. Confounding effects of season. It is predicted that larger flocks will form in mid-winter because more redshanks are present on the estuary during this period.

Secondly, redshank feeding behaviour will also be evaluated and this will measure three traits, steps, feeding effort and feeding success. Predictors such as temperature, tidal influence, distance from the saltmarsh boundary, flock size, vegetation habitat and *O. gammarellus* density, and distance from the nearest creek edge will tested against each behaviour trait.

27. Steps. It is hypothesised that step rate will decrease in more profitable areas (denser *O. gammarellus* patches) where feeding effort is more concentrated and birds spend more time foraging. Similarly, it may decrease in denser areas of vegetation such as *F. rubra*.

28. Feeding effort. Measured by probe rate, where redshanks purposefully stop and focus on probing a specific patch. It is predicted that in certain types of vegetation, feeding effort will increase because redshanks will forage for *Orchestia* by touch (*e.g.* dense vegetation such as *F. rubra*), rather than peck at the surface where they are likely to be feeding visually.

29. Feeding success. Measured by swallow rate. It is predicted that this will increase in denser areas of *O. gammarellus*, but it may be reduced by interference competition and where prey activity is depressed. It is predicted that swallow rate may also increase in colder temperatures as there is a need for redshanks to increase their energetic intake to reduce the threat of starvation.

4.2 Methods

4.2.1 Measuring the influences on redshank flock size

Influences on redshank flock size address objectives 21 to 26. Flock size was evaluated during the same fieldwork phases (winters 2 and 3) and using the same raw data (Table 3.2) and methodology for measuring redshank feeding distribution (3.2.2), where observations were recorded along with day number, weather and high tide measurements. Distance of each redshank observation to the saltmarsh boundary was calculated in ArcGIS (ESRI, 2013) using proximity analysis (Arc toolbox>Analysis Tools>Near>Input = redshank observation points>Near Features = saltmarsh boundary edge). In addition, the *O. gammarellus* density data from the *Orchestia* density index (Figure 3.3 left, page 90), which had previously been produced in ArcGIS (ESRI, 2013), and used for evaluating redshank feeding presence in relation to *Orchestia* density, was entered in the model as a continuous variable where each density level ranged from 1 - least dense to 8 - most dense. Vegetation type could not be categorised due to the large distance between flocks and the observer, which could be up to 200m away from the nearest bird. Therefore, a further variable was constructed called *vegetation habitat type*, where redshanks were categorised as feeding in one of four types of dominant vegetation. These were 1 - *F. rubra*, 2 – *F. rubra*/*A. maritima* mixed, 3 – *A. maritima*, and 4 – *P. maritima*. To achieve this each vegetation area boundary was walked and plotted using the handheld GPS, the points were then downloaded into ArcGIS (ESRI, 2013), and a vegetation area polygon was digitised by joining the points. The redshank feeding observation points were then placed over this base layer to determine the vegetation habitat type for each point. For the statistical analysis, the response variable, flock size, was converted to the natural log which produced a normal distribution, so a linear model was run.

4.2.2 Measuring redshank feeding behaviour

Redshank feeding behaviour was broken down to measure steps, probes (effort) and swallows (success), described in objectives 27 to 29. Redshank foraging on the saltmarsh was videoed using a tripod mounted Sony CX405 Handycam. The fieldwork was carried out in winter 3 on selected days (15) between 19 Jan and 8 Mar. In all, 149 focals were taken from a few seconds to over 20 minutes in length (mean 70 seconds ± 3.8 SE), focusing on a selected bird until it flew off or went out of view (*e.g.* into a creek), after which another bird was then selected. The mean number of focals per day was 8.2 ± 1.6 SE, and the mean number of birds per focal 18.5 ± 5.3 SE. However, flock sizes were usually small so the same bird may have been videoed numerous times in one day. The estimated distance to the nearest creek, flock size, and vegetation type that the bird was foraging in was noted, then classified in accordance with the categories as per 4.2.1. On playback, the number of steps, pecks, probes and swallows per minute were counted. Pecks appeared to be simply an exploratory reactive movement to a visual stimulus that might or might not be worthy of further investigation by probing, and rarely resulted in a swallow. It was therefore decided to measure feeding effort by the number of probes per minute because it was generally probing which led to a swallow. A swallow was interpreted as a successful prey capture (success rate). Dissimilarity-based analysis was used initially and an NMDS diagram plotted using the R package ecodist (Goslee and Urban, 2007), to give some indication of which feeding behaviour was associated with which vegetation habitat type. Feeding behaviour was modelled using GLMMs contained in R package lme4 (Bates, 2010) where day number and focal clip were entered in as random effects. R package lmerTest (Kuznetsova *et al*., 2016) was

used to obtain *p* values for models constructed in lme4 which are not shown in model summary tables for this package. Because air temperature and soil temperature were collinear in the success rate model, they were modelled separately. In the other models, they were removed early in the analysis because they produced non-significant effects.

4.3 Results

4.3.1 How flock size varies – objectives 21-26

The data collected for this part of the research are detailed in Tables 4.1 and 4.1.

Table 4.1 *Data for abiotic variables collected from 316 redshank observations (winter 2 = 200, winter 3 = 116), where mean flock size in winter 2 was 17.54 (SE ± 0.61) and was 4.65 (SE ± 0.24) in winter 3.*

	Winter 2		Winter 3	
Abiotic predictor variables	Mean	SE	Mean	SE
Air temperature (ºC)	5.16	0.21	5.43	0.15
Soil temperature (ºC)	3.53	0.20	5.90	0.15
Wind speed (mph)	3.17	0.27	4.65	0.44
Distance to boundary (m)	34.30	2.50	39.22	2.77
High tide height (m)	5.00	0.04	4.63	0.04
High tide time (decimal)	12.63	0.22	10.96	0.26
Time to/from nearest high tide (decimal)	3.19	0.10	2.72	0.12

Table 4.2 *Data for biotic variables collected from 316 redshank observations (winter 2 = 200, winter 3 = 116), where mean flock size in winter 2 was 17.54 (SE ± 0.61) and was 4.65 (SE ± 0.24) in winter 3.*

		Winter 2			Winter 3		
Biotic predictor variables		*N* birds observed	Mean	SE	*N* birds observed	Mean	SE
Vegetation habitat type	*F. rubra*	556	16.35	1.18	48	6.86	1.06
	F. rubra/A. maritima mixed habitat	410	15.77	1.36	156	5.78	0.53
	A. Maritima	1917	17.92	0.87	317	4.12	0.26
	P. maritima	626	18.97	1.68	19	3.80	0.92
O. gammarellus density index	1	406	23.88	2.78	12	6.00	4.00
	2	471	18.12	1.40	38	6.33	1.96
	3	1094	16.83	1.18	140	5.00	0.40
	4	589	15.50	0.90	150	4.84	0.51
	5	436	21.80	1.88	62	3.65	0.53
	6	261	14.50	1.53	53	4.42	0.71
	7	112	18.67	3.48	42	4.67	0.60
	8	140	14.00	1.91	43	3.91	0.51

Redshank feeding flock sizes were compared against predictors including weather, flock distance to the saltmarsh boundary species of vegetation (habitat type) and *O. gammarellus* density from winter 1 using the density area index. High tide height, time to the nearest high tide, and day number were also included as confounding variables. Flock sizes were much smaller in winter 3 and out of 116 observations of feeding flocks, on only four occasions was the flock size greater than 10 birds (10, 11, 13 and 15) and mean flock size was 4.65 birds (SE ±

0.24). When compared to winter 2 data, from 200 observations 166 of these had flocks of between 10 and the maximum of 49 birds (mean 17.54 birds, SE ± 0.61)

Weather – objective 21

Flock size increased as air temperature increased from 8.5 to 15 birds per flock in winter 2 and from 2 to 3.5 birds in winter 3 (air temperature: min 0.4°C, max 13.5°C). Soil temperature showed a negative quadratic effect where in winter 2 there was a decrease in flock size as soil temperature increased from 24 birds at 0°C down to 11 birds at 7°C, before increasing to 12 birds at 9.1°C. For winter 3 and across the same temperature range this was just under 6 birds decreasing to 2.7 birds, increasing to just under 3 birds. There was an effect of wind speed with an increase in flock size of 9 to 18 birds in winter 2 and 2 to 4 birds in winter 3, as wind speed rose from 0 mph to 16.1 mph (Table 4.3, Figure 4.1). The prediction that as temperatures fall flock size increases, although true for soil temperature, was not true for air temperature where the opposite occurs and flock sizes are larger as air temperature increases. The prediction that flock size increases along with wind speed was shown to be true.

Distance from the saltmarsh boundary edge – objective 22

Distance of the flock to the saltmarsh boundary showed a negative marginally significant effect where initially, flock size decreased sharply from the boundary edge to around 5m in, but was then followed by a more gradual decrease out to the maximum distance of 181m. The overall decrease in flock size was 12.7 to 9.5 birds in winter 2 and 3 to 2.3 birds in winter 3 (Table 4.3, Figure 4.1). Therefore, the prediction that flock sizes increase close to the boundary of the saltmarsh where predators and especially sparrowhawks are likely to be hiding was not supported.

Vegetation habitat type and O. gammarellus density – objectives 23 and 24

Vegetation habitat type and *O. gammarellus* density index variables were removed from the linear model because they showed no significant effect (Table 4.3). The hypothesis that flock size should be larger in vegetation where *O. gammarellu*s is more likely to be present and abundant (*e.g. F. rubra*), and in vegetation where redshanks are more likely to be present (*i.e. A. maritima*) was not supported. Similarly, neither was the hypothesis that flocks should be larger in areas of greater *O. gammarellus* density.

The effects of tide – objective 25

There was a decrease in flock size as high tide heights increased. In winter 2 this was from just over 13 birds when the nearest high tide was at 4m to just under 8 birds when this was 5.7m. In winter 3, between the same tide heights this was 3 birds down to 2 birds (Table 4.3, Figure 4.1). Therefore, the prediction that flock size should be greater when high spring tides force redshanks into reduced areas of saltmarsh was not proven where in fact the opposite occurs. Hence flocks were larger when more marsh is available for foraging during low neap high tides.

There was a positive marginally non-significant effect for time to/from the nearest high tide where flock size increase in winter 2 was 8.5 to 12.5 birds and in winter 3, 2 to 3 birds (time of nearest high tide: min 0625 hrs,

max 1750 hrs) (Table 4.3, Figure 4.1). Therefore, the prediction that as time to the nearest high tide reduces flock size becomes larger because birds are forced into reduced areas of marsh was not proven.

The effects of season – objective 26

Day number showed a negative quadratic effect where in winter 2 there was a decrease in flock size from 20 to just under 10 birds before an increase up to 18 birds. In winter 3 this reduction was from just under 5 down to 2.3 birds increasing to 4.3 (first day – day 12, 23 November; last day – day 119, 9 March). However, the regression was heavily influenced by large flock sizes at the beginning of winter 3 followed by no flocks at all until the second week in January, therefore the plot is not illustrated (Table 4.3). Nevertheless, the prediction was supported that flocks are larger in midwinter.

Table 4.3 *Redshank feeding flock size for winters 2 and 3. The response variable flock size was transformed to the natural log as was the predictor variable, flock distance to the saltmarsh boundary.*

Variable	Estimate (Log)	SE (Log)	*t*	*P*
Intercept (including winter 2)	5.14	0.54	9.5	**<0.001**
Winter 3	-1.43	0.07	-18.9	**<0.001**
Air temperature	0.04	0.01	3.1	**0.002**
Soil temperature	-0.22	0.05	-4.5	**<0.001**
Soil temperature^2	0.02	0.01	3.7	**<0.002**
Wind speed	0.04	0.01	5.4	**<0.001**
Flock distance to saltmarsh boundary (log)	-0.05	0.03	-1.8	0.075
High tide height	-0.31	0.11	-2.9	**0.004**
Time of nearest high tide	0.03	0.02	1.9	0.063
Day number	-0.02	0.01	-5.0	**<0.001**
Day number^2	0.01	0.01	5.2	**<0.001**

Significant *P*-values marked in bold. The adjusted R^2 for this model is 0.69. Degrees of freedom 305. Full model AIC: 454, best model AIC: 438. Variables removed from full model – vegetation habitat type, *O. gammarellus* density index^2, *O. gammarellus* density index, air temperature^2, wind speed*air temperature, *O. gammarellus* density index*soil temperature, *O. gammarellus* density index*air temperature, *O. gammarellus* density index* Flock distance to saltmarsh boundary (log), *O. gammarellus* density index*vegetation habitat type.

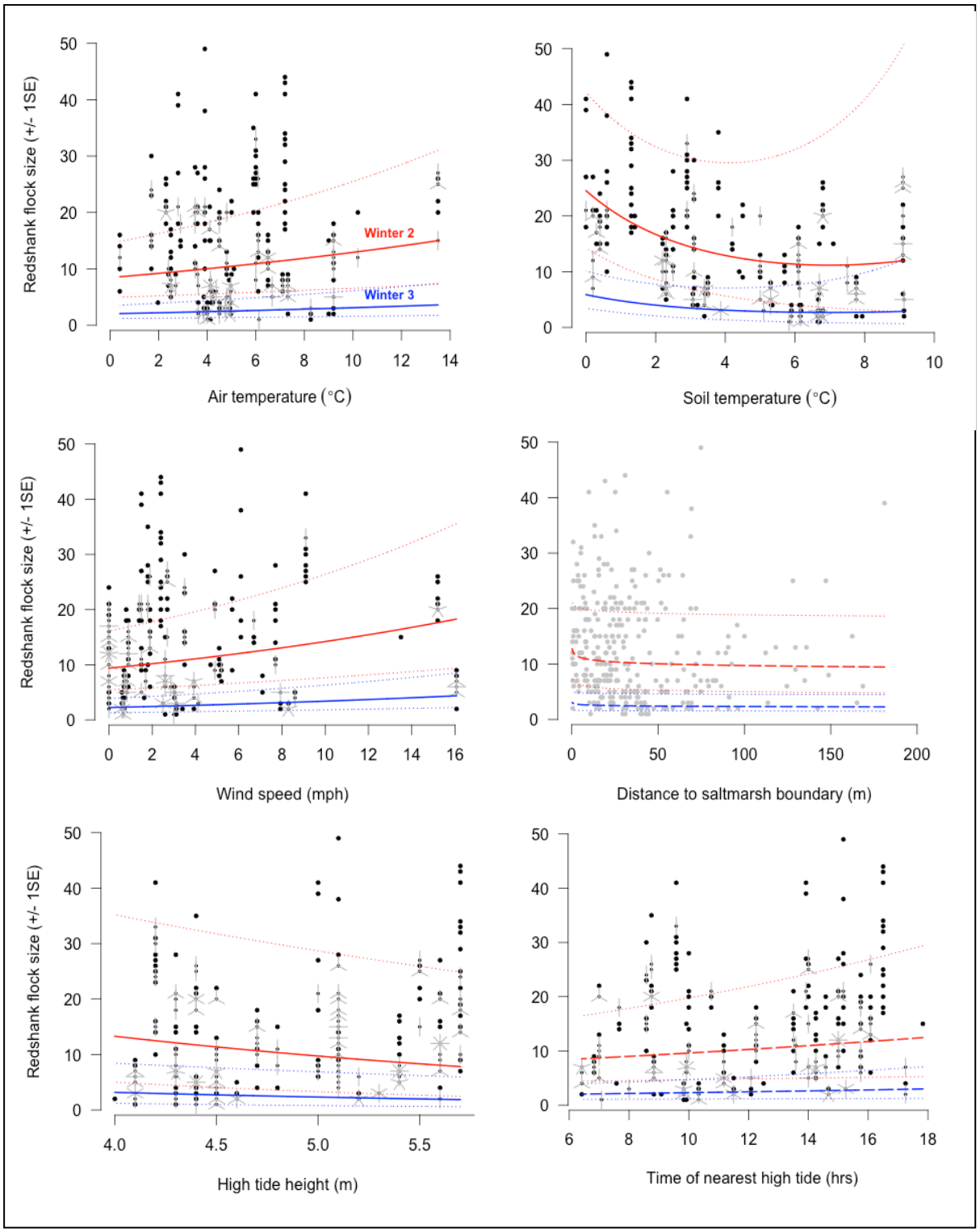


Figure 4.1 *Results from the best linear model showing feeding redshank flock size and its relationship to abiotic variables of air temperature (top left), soil temperature (top right) wind speed (centre left), distance of the flock to the saltmarsh boundary - marginal significant effect (centre right), high tide height (bottom left) and time to the nearest high tide- marginal significant effect (bottom right). Redshank feeding data for winters 2 and 3 shown from a total of observations = 316. Parameter estimates and SEs plotted from the model in Table 4.3.*

4.3.2 Variation in redshank feeding behaviour – objectives 27-29

The data for this section are detailed in Table 4.4.

Table 4.4 *Raw data for objectives 27-29 from 149 redshank focals recording step, probe (effort) and swallow (success) rates, on 15 days between the 19 Jan and 8 Mar in winter 3.*

Continuous predictor variable	Mean	SE
Air temperature °C	5.89	0.10
Soil temperature °C	6.72	0.07
Distance to saltmarsh boundary edge (m)	42.93	1.91

Categorical predictor variable	Mean steps/min	SE	Mean probes/min (effort)	SE	Mean swallows/min (success)	SE
O. gammarellus density index						
Level 1 (lowest density)	83.06	15.23	4.37	1.10	0.00	0.00
Level 2	74.78	12.24	1.78	0.46	0.17	0.09
Level 3	74.82	4.77	5.83	0.76	0.76	0.18
Level 4	63.20	3.97	5.63	0.61	0.76	0.13
Level 5	59.53	4.48	5.17	0.64	0.93	0.21
Level 6	70.73	5.51	6.11	0.71	1.16	0.28
Level 7	65.85	7.72	3.66	0.58	0.81	0.25
Level 8 (highest density)	69.91	23.15	2.10	0.93	0.27	0.22
Vegetation habitat type						
A. maritima	97.40	6.31	2.24	0.48	0.08	0.04
F. rubra	54.30	3.47	8.58	0.59	1.85	0.23
F. rubra/A. maritima mixed	67.63	2.95	5.04	0.44	0.56	0.09
P. maritima/A. maritima mixed	87.14	16.46	2.23	0.86	0.39	0.33
P. maritima	73.53	8.27	5.43	0.77	0.38	0.14

Species of vegetation and their association with feeding behaviour

An NMDS plot of the redshank feeding behaviour in different vegetation habitats (pecks/min, probes/min, swallows/min and steps/min), showed that probe and swallow rates were greater in areas of *F. rubra* and the *F. rubra*/*A. maritima* mixed habitat, but peck rate was less. Step rate was greater in areas of *A. maritima P. maritima* and *P. maritima*/*A. maritima* mixed habitat (Figure 4.2).

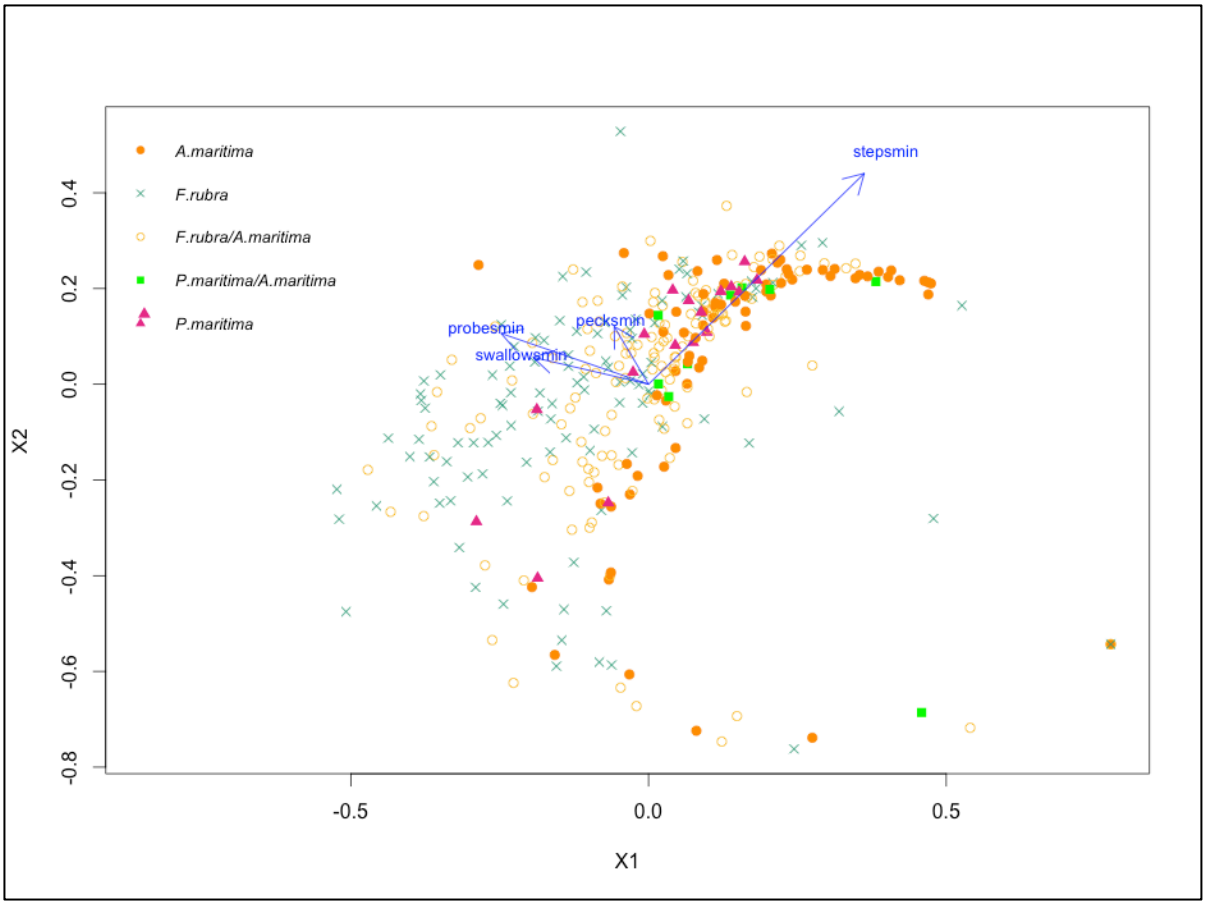


Figure 4.2 *NMDS scaling diagram feeding behaviours and their separation distances in 2-dimensional space in 5 types of vegetation habitat.*

Redshank steps – objective 27

Step rate was measured in certain types of habitat, and in different *O. gammarellus* density areas. Because air temperature and soil temperature were collinear, they were modelled separately, but neither of them showed a significant effect and were removed from their respective models. Step rate showed a positive relationship with the *O. gammarellus* density index in habitats of *F. rubra*, *F. rubra*/*A. maritima* mixed habitat and *P. maritima*, but the step rate was reduced in comparison with *A. maritima* (Table 4.5 Figure 4.3). Therefore, the hypothesis that step rate decreases when *O. gammarellus* density is higher was proved incorrect where the opposite is the case and step rate increased along with density. However, step rate was greater in the shorter more open vegetation of *A. maritima* and in mixed habitats containing this species. In denser grasses *F. rubra* and *P. maritima* the step rate was reduced by comparison.

Table 4.5 *Best GLMM for redshank step rate. O. gammarellus density index = 1 least dense, 8 = densest. Steps/min transformed to the square root. Because air and soil temperature were collinear, models for each were run separately, but both were dropped from the model because there was no significant effect.*

Variable	Estimate	SE	*t*	*P*
Intercept (*A. maritima*)	7.01	0.78	9.0	**<0.001**
Habitat - *F. rubra*	0.52	1.14	0.4	0.647
Habitat - *F. rubra*/*A. maritima* mix	1.90	0.91	2.1	**0.039**
Habitat – *P. maritima*/*A. maritima* mix	3.01	5.69	0.5	0.597
Habitat – *P. maritima*	3.50	2.21	1.6	0.114
O. gammarellus density index	0.49	0.16	3.1	**<0.001**
Habitat - *F. rubra***O. gammarellus* density index	-0.55	0.24	-2.3	**0.021**
Habitat - *F. rubra/A. maritima***O. gammarellus* density index	-0.68	0.19	-3.5	**<0.001**
Habitat – *P. maritima/A. maritima***O. gammarellus* density index	-0.68	1.09	-0.6	0.532
Habitat – *P. maritima***O. gammarellus* density index	-1.42	0.64	-2.2	**0.027**

Significant *P* values marked in bold. R^2 variance explained by random factors = 0.21, R^2 variance explained by fixed effects = 0.10, total = 0.31. AIC: 1574 full model, AIC: 1534 best model. Variables removed from full model – air temperature, distance to saltmarsh boundary, flock size, distance from nearest creek edge, *O. gammarellus* density index*air temperature, *O. gammarellus* density index*distance to saltmarsh boundary, air temperature*flock size. Degrees of freedom = 344.

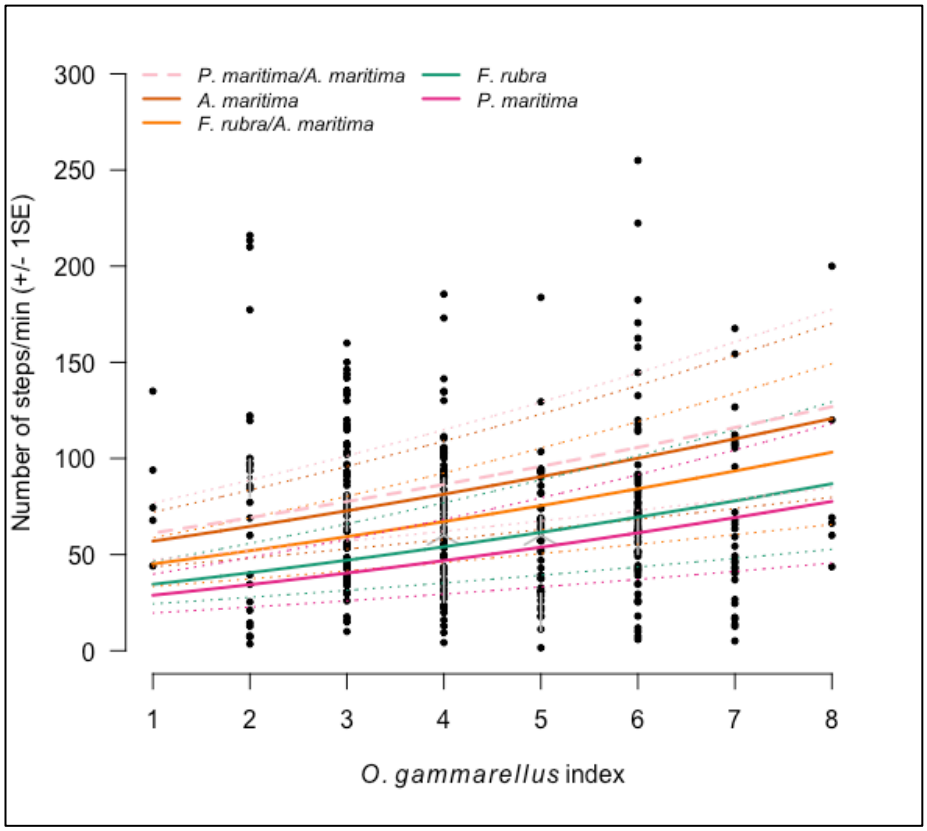


Figure 4.3 *Step rate against O. gammarellus density. 1 = lowest density, 8 = highest. P. maritima/A. maritima mixed habitat showed no significant effect and is indicated by the dashed line. Parameter estimates and SEs plotted from the model in Table 4.5.*

Redshank feeding effort – objective 28

Soil and air temperature were again modelled separately due to collinearity, but were removed because neither showed a significant effect. Therefore, both models converged to produce the same best model. Over 75% more effort was put into feeding in *F. rubra* rather than *A. maritima* (intercept) which was 2.7 to 4.6 probes/min. *F. rubra/A. maritima* mixed habitat also showed a significant effect with a 49% increased effort compared to *A. maritima*, which was 2.7 to 4 probes/min (Table 4.6, Figure 4.4). The prediction that redshank feeding effort increases in denser vegetation such as *F. rubra* was supported.

Table 4.6 *Best GLMM model for redshank feeding effort (probe rate). Response variable probes/minute (effort expended) transformed to the natural log.*

Variable	Estimate	SE	*t*	*P*
Intercept (*A. maritima*)	0.99	0.18	5.6	**<0.001**
Habitat - *F. rubra*	0.70	0.14	4.9	**<0.001**
Habitat - *F. rubra/A. maritima*	0.28	0.13	2.1	**0.034**
Habitat - *P. maritima/A. maritima*	-0.25	0.33	-0.7	0.450
Habitat - *P. maritima*	0.37	0.23	1.6	0.104

Significant *P* values are marked in bold. R^2 variance explained by random factors = 0.36, R^2 variance explained by fixed effects = 0.10, total = 0.46. AIC: 659 full model, AIC: 607 best model. Variables dropped from full model – air temperature, soil temperature, distance to saltmarsh boundary, flock size, distance from nearest creek edge, *O. gammarellus* density index*vegetation habitat type, distance to saltmarsh boundary**O. gammarellus* density index, air temperature*flock size, soil temperature*flock size. Degrees of freedom = 274.

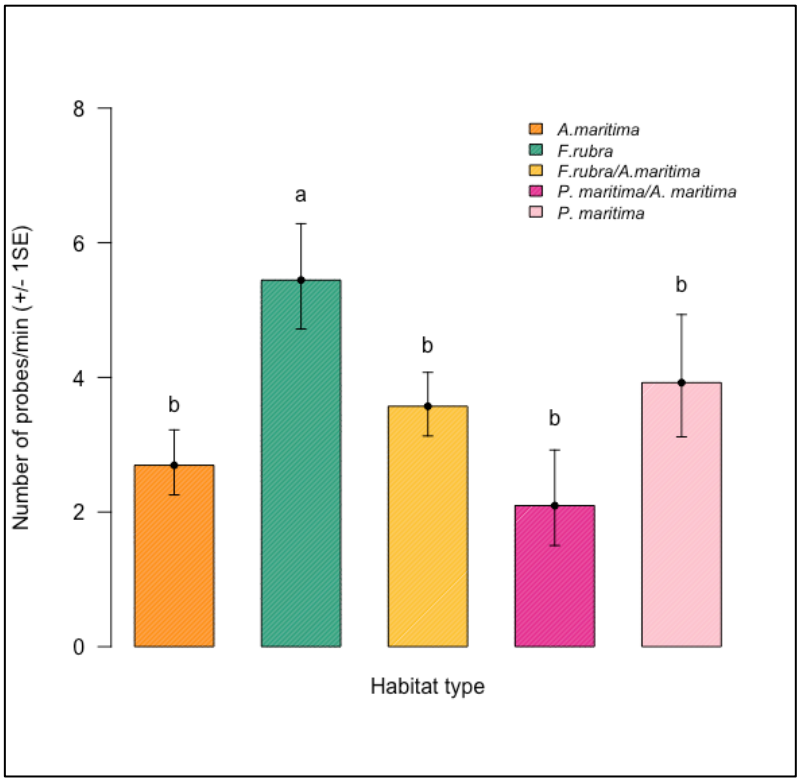


Figure 4.4 *Feeding effort (probe rate). Specific post-hoc tests were carried out for the GLMM using the multcomp package and the same letters indicate no statistically significant difference between those variables. The results showed that F. rubra was significantly different from the other four types of vegetation. Parameter estimates and SEs plotted from the model in Table 4.6.*

Redshank feeding success – objective 29

The independent models for air and soil temperature (modelled separately due to collinearity), showed that the two temperatures were the only variables that showed a significant effect in their respective best models. There was an increase in swallows/minute from just over 1 to 2.5 with an increase in air temperature between 3.4 and 9.7°C, whereas for soil temperature the increase was just under 1 to just over 2 swallows/minute between soil temperatures of 3.1 and 8.9°C. The *O. gammarellus* density index, flock size, vegetation type and distance to the saltmarsh boundary were all entered in the models but were dropped because they showed no significant effect (Table 4.7, Figure 4.5). Therefore, the prediction that swallow rate will increase in denser areas of *O. gammarellus* was incorrect, but it does increase when air and soil temperatures are colder.

Table 4.7 *Best GLMM models for redshank feeding success (swallow rate), air temperature and soil temperature (separate models). Response variable swallows/minute transformed to the natural log.*

Variable	Estimate (Log)	SE (Log)	*t*	*P*
Intercept	-0.32	0.27	-1.2	0.248
Air temperature	0.13	0.04	2.8	**0.013**
Intercept	-0.72	0.49	-1.5	**0.165**
Soil Temperature	0.17	0.07	2.3	**<0.040**

Significant *P* values are marked in bold. Day number and focal clip entered as random effects. Variance caused by fixed effects: air temperature = 0.10, soil temperature = 0.08. Variance caused by random effects: air temperature = 0.34, soil temperature = 0.35. Full air temperature model AIC: 342, best model AIC: 280. Full soil temperature model AIC: 338, best model AIC: 281. Variables removed from full air temperature model: habitat type, *O. gammarellus* density index, distance to the saltmarsh boundary, distance from nearest creek edge, flock size, *O. gammarellus* density index*air temperature, *O. gammarellus* density index*vegetation habitat type, *O. gammarellus* density index*distance to the saltmarsh boundary, air temperature*flock size. Variables removed from full soil temperature model: vegetation habitat type, *O. gammarellus* density index, distance to the saltmarsh boundary, flock size, *O. gammarellus* density index*soil temperature, *O. gammarellus* density index*vegetation habitat type, *O. gammarellus* density index*distance to the saltmarsh boundary, soil temperature*flock size. Degrees of freedom for both models = 128.

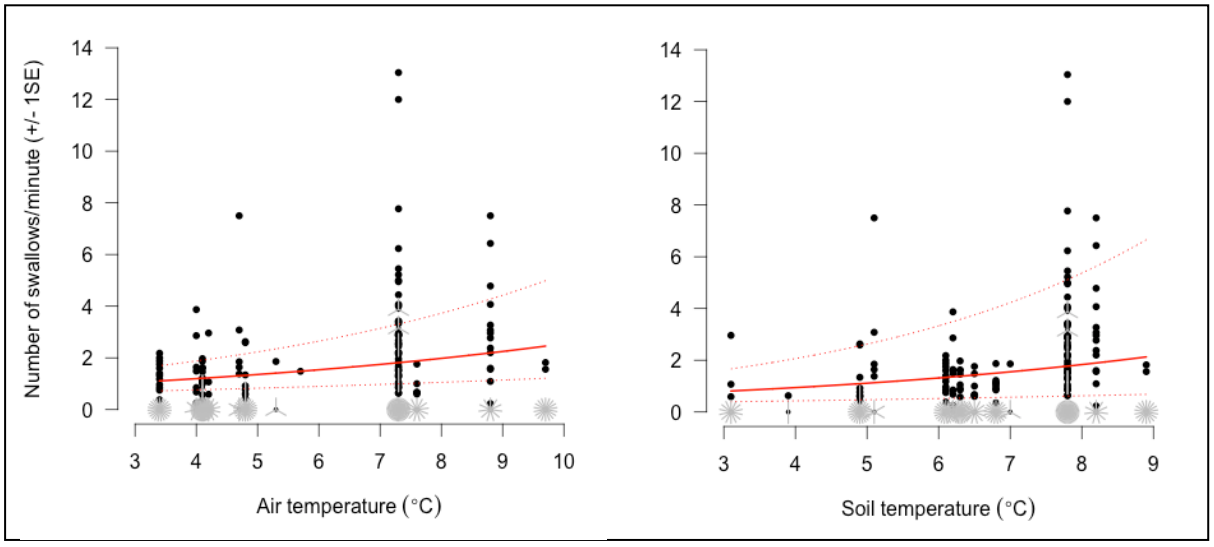


Figure 4.5 *Success rate (swallows/minute) against temperature. Plots taken from two separate models where air and soil temperature were modelled independently, but each was left as the only variable showing a significant effect. Air temperature min = 3.4°C, max = 9.7°C; soil temperature min = 3.1°C, max = 8.9°C Parameter estimates and SEs plotted from the model in Table 4.7.*

4.3.3 Summary of results

Higher air and soil temperatures resulted in an increase in flock size on the saltmarsh, but this was also evident at low soil temperatures. Flock sizes of foraging redshanks increased in windier weather. An increase in flock size with a reduction in distance to the saltmarsh boundary showed a marginally non-significant effect where flock size was larger at the edge before a steep reduction up to 5m from the edge, followed by a very gradual decrease towards the inner marsh. Flock size showed no significant relationship to the density of *O. gammarellus*. Flock size was not larger during spring high tides when uncovered saltmarsh area was at a minimum, and during the spring low tide when a larger foraging area of saltmarsh and mud was available. Similarly, an increase in flock size with a reduction in time to the nearest high tide was marginally non-significant. Flock sizes were also larger from mid-January until the end of February.

The results of redshank foraging behaviour show that their steps increased along with an increase in *O. gammarellus* density, but this was not the same in all habitats. Steps were fewer in denser saltmarsh grasses such as *F. rubra* and *P. maritima*, whereas steps increased in more open *A. maritima* and *A. maritima*/*F. rubra* mixed habitat. Feeding effort measured by probe rate, indicated that effort increased in *F. rubra* and *F. rubra*/*A. maritima* mixed habitat compared to other types of vegetation, whereas success (swallow rate), increased as air and soil temperatures rose.

4.4 Discussion

4.4.1 The effects of weather on flock size

Wind speed

Although there was no significant effect on the probability of redshanks feeding on the saltmarsh at higher wind speeds (page 88), which disagrees with Yasue, *et al*. (2003), in contrast when redshanks were present on the saltmarsh, flock size increased with wind speed. The reason for this might be that higher wind speed causes redshanks to move from the estuary to the shelter of the saltmarsh to feed on *Corophium* in the creeks, and in doing so they were hidden from view, so their presence was not recorded. If this coincides with cold mud temperatures, *Corophium* become less available as already detailed (page 109), and redshanks move onto the saltmarsh vegetation to feed on *Orchestia* because they are nearby and an energy-rich food source (Cresswell and Whitfield, 2008). An alternative feeding ground would be on the eastern rocky shore which also offers shelter and a reduced predation risk, but this is inhabited by adult redshanks, which exclude juveniles which are then forced onto the saltmarsh to feed (Cresswell, 1994a). Switching to the saltmarsh, redshanks are first prioritising starvation as the immediate threat, more birds congregate, and foraging here rather than in the creeks offers some shelter from the wind especially close to Little Binning Wood on the western edge. Second, they may trade-off the risk of feeding on the saltmarsh associated with the increased threat from sparrowhawk predation, by forming larger flocks so that vigilance, and confusion and dilution effects are enhanced (Cresswell, 1994b; Hilton, Cresswell and Ruxton, 1999); Lind and Cresswell, 2005; Quinn and Cresswell, 2005) (Figure 4.6).

Air temperature

As air temperature increased on the saltmarsh, so did flock size. This appears contradictory because at higher air temperature, intake rates do not need to be as great due to a reduction in redshank energy requirements (Davidson, 1981; Davidson and Evans, 1982), although it is possible that extensive cold periods may require redshanks to continue building up depleted fat reserves at the onset of warmer weather (Dugan *et al*., 1981; Mitchell *et al*., 2000), so intake rates may be higher for a time after a colder period. One possible explanation might be that *Orchestia* activity increases at higher air temperature, this may make them more visible which provokes a feeding response from redshanks. A model describing similar temperature related activity by prey and its impact upon predators was illustrated by Logan *et al*. (2006), where predation rates by wolf spiders (Lycosidae) were increased on grasshoppers when these become more active at higher temperatures. In effect, increases in temperature dictate if and when predation events take place (Logan and Wolesensky, 2007). Also, *Orchestia* are more likely to be found in vegetation such as *F. rubra* that occurs adjacent to creek edges, and increased activity means that they may inadvertently fall into creek mud (pers. obs.). This could trigger a reaction and act as a cue for redshanks which then switch feeding to saltmarsh vegetation, where feeding rate might be increased resulting in larger flocks forming. This means that redshanks can be less vigilant, spend more time foraging (Cresswell and Whitfield, 2008), and may temporarily facilitate the intake of conspecifics by disturbing escaping *Orchestia* into the vicinity of a neighbouring bird. In larger flocks, redshanks might be able to feed closer to the saltmarsh boundary in *O. gammarellus*-rich areas that were previously out of bounds to them due to increased predation threat (Cresswell, 1994b). However, flock size and distance to the saltmarsh boundary showed a marginally non-significant effect

and flock size only increased dramatically less than 5m in from the edge, even though Cresswell (1994b) found that redshanks were at much greater risk within 50m of the boundary edge. *Orchestia* are better able to escape at higher air temperatures because they jump and crawl more and their reactions are quicker. Therefore, disturbed *Orchestia* may come within the vicinity of a neighbouring redshank for the first few seconds of activity (10 - 20 seconds), before hiding in the soil or under vegetation. It is at this point that *Orchestia* are depressed and redshanks move to another patch to feed, so that redshank residence time in a feeding area is dependent on the onset of *Orchestia* depression, which may be from a few minutes to several hours Despite earlier results, larger flocks may thus increase interference competition where foraging disturbance depresses *Orchestia* numbers, decreasing intake rate, rather than increasing it, and resulting in redshanks moving onto another patch. Nilsson and Ruxton (2004) suggested that a positive feedback was the result, where interference between predators due to abiotic change such as an increase in temperature making more prey active, resulted in them foraging less, decreasing the predation risk which benefited prey survival. However, at higher air temperature, energetic needs are lower and redshanks probably reach the optimal intake with less feeding effort, so interference competition between birds may be reduced (Figure 4.7).

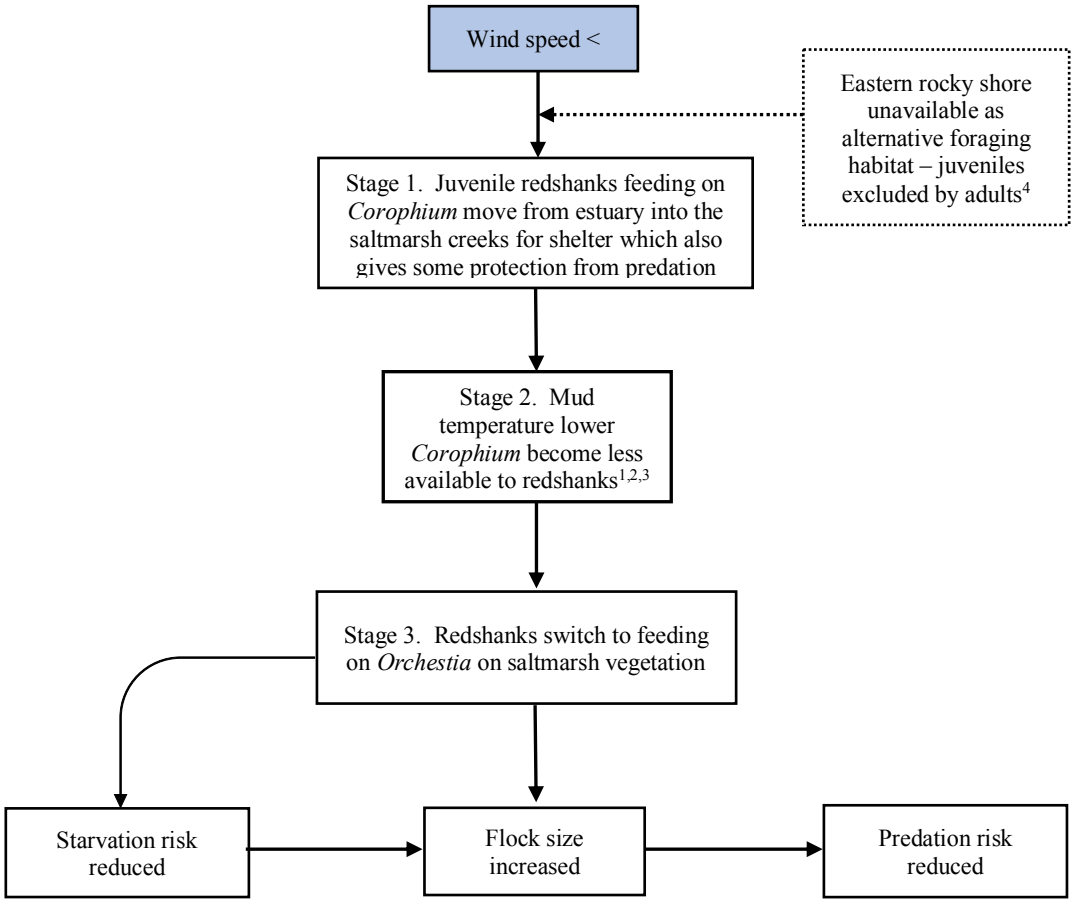


Figure 4.6 *Wind speed and its effect on choice of redshank feeding habitat. Stage 1 - increased wind speed results in juvenile redshanks moving from the open estuary into saltmarsh creeks for shelter and some degree of protection from sparrowhawks. They continue to feed on Corophium. Stage 2 - when wind speed is high and mud temperature falls, Corophium become less available. Stage 3 - redshanks switch habitat to saltmarsh vegetation, which satisfies their energetic requirements, and the immediate risk of starvation is averted. Larger flocks form which also helps to mitigate the risk of predation through vigilance, and the escape benefits of confusion and dilution. Original concepts except where indicated by the following references: 1. Meadows and Ruadh (1981), 2. Goss-Custard (1970a), 3. Cramp and Simmons (1983), 4. Cresswell (1994a).*

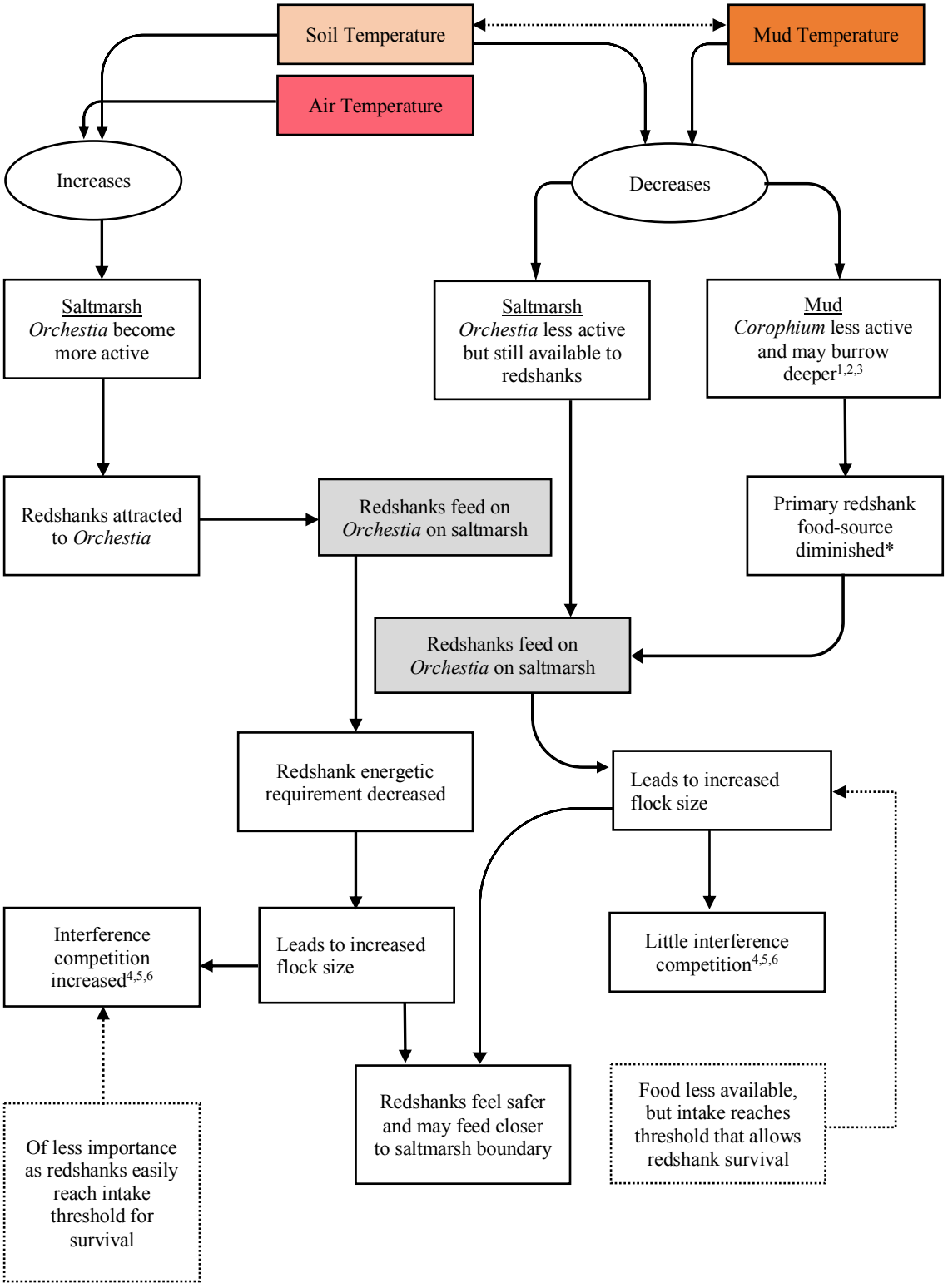


Figure 4.7 *Air and soil temperatures and their effect on feeding redshanks. Higher air and soil temperatures lead to an increase in flock size, because Orchestia are more active and therefore conspicuous. Intake rates may increase as Orchestia escape from one bird into the vicinity of neighbouring birds. Interference competition could be the result and Orchestia availability may become depressed, before redshanks move on to the next patch. Low soil temperatures also result in larger flocks possibly because Corophium become less available and Orchestia become the primary food source. Although they are difficult to detect they satisfy a redshanks energetic needs and interference competition is less likely to occur. Original concepts except where indicated by the following references: 1. Meadows and Ruadh (1981), 2. Goss-Custard (1970a), 3. Cramp and Simmons (1983), 4. Krause and Ruxton (2002), 5. Minderman et al. (2006), 6. Cresswell and Whitfield (2008). * A subject that could form the basis of future research.*

Soil temperature

Soil temperature had a negative quadratic effect with higher flock sizes at the lowest and highest temperatures. The consequences of redshank feeding behaviour at higher air temperature as described above, also probably applies to higher soil temperature. At lower soil temperature flock size increases probably because fewer *Corophium* are available in the creeks and on the estuary, so *Orchestia* on the saltmarsh are the only major food source available for juvenile redshanks which are excluded from the safer eastern shore by adults. A similar example of habitat switching by waders was detailed by Furnell and Hull (2014), where on the north Yorkshire coast, turnstone (*Arenaria interpres*), oystercatchers and redshanks switched habitats in winter from sandy and rocky shores to adjacent cliff tops, especially golf courses and recreational parks, to forage in short grassland which had a higher invertebrate population than nearby agricultural pasture. They suggested that the reason for this was to maximise intake rates and stave off the threat of starvation in severe weather conditions (Furnell and Hull, 2014). However, there was no mention in the research of invertebrates on the shore becoming unavailable due to colder temperatures as the reason for the waders switching habitats. Nevertheless, flock size on the saltmarsh increases despite redshanks having difficulty in detecting *Orchestia* which are less active and conspicuous in colder soil temperatures, and although their intake rate is probably reduced because of this, it must reach a level that satisfies their energetic requirements. If *Orchestia* are less active, interference competition between redshanks is probably averted (Figure 4.7).

Other considerations regarding redshanks switching foraging to the saltmarsh

Other factors apart from weather conditions may influence switching of feeding habitat to the saltmarsh and flock size increases. *Corophium* are more active on the surface of mud on the ebb tide (Watkin, 1941; Morgan, 1965) and waders such as semipalmated sandpiper (*C. pusilla*) (Beauchamp, 2006) and redshank (Goss-Custard, 1970a) feed more intensely on them at this time. *Corophium* tracks leading to burrows are also more visible on the surface of the mud following tidal inundation, which may act as a cue for feeding waders (Zwarts and Wannik, 1993). If *Corophium* availability then decreases (*i.e.* surface movements are reduced), they may become less available to predators such as redshank which then need to find an alternative prey, in this case *Orchestia*. Also, Goss-Custard (1970a) found that redshanks walking on the mud surface can depress *Corophium* which become temporarily unavailable requiring them to switch habitats. In the November of winter 1, a tidemark of dead *Corophium* was found at the study site that stretched along the main creek from its mouth for about 150m. Temperatures were at seasonal norm at this time, so cold conditions may not have been the cause, which might have been due to a pollution event, although no evidence of this could be found. This would undoubtedly have reduced *Corophium* biomass in the main creek, and may have impacted on redshank intake, although this was not measured at the time. Therefore, stochastic events like this may cause redshanks to switch habitats.

4.4.2 Redshank feeding behaviour

Steps

The preliminary NMDS scaling diagram indicated that there is some association between the number of steps and vegetation where step rate increases in *A. maritima*, *P. maritima,* and possibly in *A. maritima/F. rubra* and *P.*

maritima/*A. maritima* mixed habitats. A lower step rate was indicated in *F. rub*ra. This was explored further so that in the best model only *F. rubra*/*A. maritima* mixed habitat and *P. maritima* showed a significant effect for step rate, which was reduced. However, critical analysis of this model needs to consider the interactions for *O. gammarellus* density index*habitat. This indicates an important association between step rate and *O. gammarellus* density which also depends on habitat type. Therefore, there is no relationship between step rate and *O. gammarellus* density for *A. maritima* and *P. maritima*/*A. maritima* mixed habitat, but there is a clear negative relationship for habitats *F. rubra*, *F. rubra*/*A. maritima* mixed habitat and *P. maritima*. This suggests that redshanks are moving quicker through *A. maritima* and *P. maritima*/*A. maritima* mixed habitat, and they are not stopping to probe and process prey, possibly because these are less profitable areas. In contrast, in *F. rubra*, *F. rubra*/*A. maritima* mixed habitat and *P. maritima*, fewer steps indicates that they are slowing down to feed, either because time is taken to process prey, because they consider this a profitable area and it is worth staying here to feed, or the structure of the vegetation (it is denser (*F. rubra*) or taller (*P. maritima*)), increases feeding time. Therefore, differences in species of vegetation and its structure would appear to affect how feeding takes place in relation to *O. gammarellus* density. However, to fully understand feeding behaviour step rate needs to be analysed in conjunction with feeding effort and feeding success.

Feeding effort

Measured by probe rate, feeding effort increased in *F. rubra* and to a lesser extent in *F. rubra/A. maritima* mixed habitat, when both were compared to *A. maritima*. This was also illustrated in the preliminary NDMS scaling diagram (Figure 4.2). In post-hoc tests *F. rubra* showed a significantly lower probe rate when compared with *A. maritima* and any mixed habitat that included this vegetation. Because *F. rubra* is a dense grass, redshanks will have difficulty in using visual cues when foraging in it and possibly also where it interfaces with *A. maritima*, a favourite foraging habitat (pers. obs.), where probing and feeling for *Orchestia* with the tip of the bill is the preferred feeding technique. This might be helped by the loose, sandy composition of soil in *F. rubr*a areas which would allow easier penetration of the thin filament-like root system of this plant, in which *O. gammarellus* especially, prefer to hide. It is likely that probing in *F. rubra* relies much more on the chance discovery of *Orchestia*, because visual cues of them are absent, hidden by thick vegetation growth. *Orchestia* appear to congregate in clusters in these root systems which would make feeding in this habitat worthwhile if one of these was discovered. However, it is suggested that blind probing is not the most profitable feeding technique here, but more a case of necessity when visual cues are absent. *A. maritima* has a very different root structure and thrives best on compacted, damp, silty soils. Its roots are thick, tightly packed and fibrous and the inflorescences are short and bulbous. It occurs in single stands, surrounded by patches of bare soil. Few *Orchestia* are present in the root systems, and neither is the increased coverage of this plant associated with greater *Orchestia* abundance (page 56). Therefore, probing in this vegetation by redshanks would be difficult and less productive. Nevertheless, the open nature of this habitat would enable redshanks to search visually and pick *Orchestia* off the surface, particularly if they were active.

Feeding success

Feeding success was measured by swallow rate and the NDMS scaling diagram indicated that this increased in *F. rubra* and *F. rubra*/*A. maritima* mixed habitat. However, the only significant associations in the best models

showed that success increased with warmer air and soil temperatures. This is probably because *Orchestia* become more active and visible to redshanks, so they could take advantage of a food resource that becomes more readily available. A crawling and jumping *Orchestia* can be grabbed or tracked and then probed for, when it escapes into the soil or vegetation. It may be that active *Orchestia* leave the relative safety of *F. rubra* and some will spill over onto *A. maritima* or the *A. maritima/F. rubra* interface areas. The short open nature of this habitat may benefit redshanks that will be hunting visually. Interference competition and prey depression may then reduce success rate, forcing redshanks to relocate onto the next patch. Increased success in warmer temperatures is less critical to the starvation threat, and increased time feeding with head up probably allows birds to be more vigilant, reducing the predation risk.

Variables that did not affect feeding behaviour

Flock size and distance to the saltmarsh boundary showed no significant effect during the research into feeding behaviour. The reason for this is probably that too few redshanks fed on the saltmarsh in winter 3, therefore a lack of variation in bird numbers meant that no meaningful measurement could be made in this winter (page 118-119). Distance from the nearest creek edge also showed no significant effect. The likely reason is that because redshanks tended to feed close to creek edges in winter 3, it was hard to determine small distances between creek edge and bird with the scope from often over 70m away. What might appear to be a redshank feeding within 1m might be 3m.

4.4.3 Conclusion

Abiotic factors such as high wind speed wind and lower temperature influence a redshank's decision to forage on the more sheltered saltmarsh. These same factors also cause redshanks to change foraging habitat from creek mud where they prey on *Corophium*, to saltmarsh vegetation where they prey on *Orchestia*. On the saltmarsh at low temperatures, feeding on *Orchestia* is driven by necessity because no other habitat is open to the mainly juvenile redshank population, but optimal foraging decisions are constrained by environmental conditions. Redshank feeding techniques must then adjust in colder temperatures when *Orchestia* are harder to find, but where the only option is to probe for them in dense grass; not a particularly successful technique that may increase predation risk because the birds use a head-down posture. In this instance starvation is the greater concern and although they are under threat from an increased predation risk, they can form larger flocks to try and mitigate this. At higher temperatures increased *Orchestia* activity stimulates a redshank feeding response, where they can optimise intake with less effort, at the same time their head-up feeding technique of pecking and grabbing, allows them to be more aware of the predation threat and enables flock sizes to increase. Flock spacing and mobility may then increase due to interference competition and prey depression, which again increases the predation threat (Minderman *et al.,* 2006). In summary, the trade-off requires redshanks to deal with the most immediate risk of starvation or predation, a decision that results in costs and benefits. These two threats are influenced by small changes in the environment outside redshank control, and affect the availability of their prey, where they feed, and their feeding technique. It is too simplistic to suggest that this is purely a bottom-up process caused by prey behaviour, because there is a causal sequence of events, most importantly changes in weather that result in redshanks constantly modifying their behaviour to survive.

CHAPTER 5. DISCUSSION

Although there has been comprehensive research into the top-down effects of this ecosystem concerning raptors and waders, specifically sparrowhawks and redshanks, the influence of other factors that are integral to the trophic structure, including bottom-up interactions, are less well understood. *Orchestia* act as a food supply for redshanks when their primary food source, *Corophium*, become less available and they move onto the saltmarsh vegetation to forage for them, but the saltmarsh represents an area of increased predation risk. *Orchestia* traits determine to a large degree how well redshanks resolve their starvation-predation risk trade-off, which will then govern the absolute and relative degree of lethal and non-lethal effects on the redshank population. Redshank feeding technique is dependent upon the type and structure of the vegetation that *Orchestia* favour, or are more able to hide in, and this may affect a redshank's ability to detect *Orchestia* and their own predators (*e.g*. sparrowhawks), because they spend more time probing in denser vegetation with head down (elevated risk), compared to barer patches where they hunt visually with head up (decreased risk). The feeding technique they use is also related to temperature, because *Orchestia* are less active in colder temperatures where they inhabit denser vegetation or burrow in the soil, but in warmer temperatures they crawl and jump more which attracts feeding redshanks to areas of less dense vegetation where they can hunt visually. For redshanks, trade-offs between starvation and predation are further impacted by increased thermoregulatory requirements in cold and windy weather, interference competition amongst conspecifics, and an increase in flock size when feeding on *Orchestia*, which enables redshanks to forage closer to sparrowhawk-concealing cover (Figure 5.1).

The results from Chapter 2 showed that of the two *Orchestia* species present on the saltmarsh, *O. gammarellus* is larger than *O. mediterranea*, and although there was no evidence that redshanks were selecting *O. gammarellus* because its larger size, they are known to be selective when choosing larger *Nereis* worms (Goss-Custard, 1977a) and *Corophium* (Goss-custard, 1967). The bias towards selecting *O. gammarellus* is, however, more likely due to other influences, particularly shorter vegetation in the outer saltmarsh where the species is most common, and which allows for easier foraging by redshanks. *O. gammarellus* males are the largest sex, so although it is possible that they are preferentially targeted, this could not be proved from this research. Therefore, a lower male composition in the population is probably not due to selective predation, but to the shorter male lifespan and/or female biased genetic selection (Ginsburger-Vogel and Charniaux-Cotton, 1982; Moore and Francis, 1986b). Saltmarsh zonation of the species is likely indicative of their tolerance to salinity and/or desiccation, with *O. mediterranea* occurring in the mid and inner marsh, where there are more tides per annum, which suggests that this species is less tolerant of desiccation, but more tolerant of salinity then *O. gammarellus*. This zonation appears to be relatively constant between years, although *Orchestia* do move with and without the aid of the tide.

The results from Chapter 3 showed that redshanks must manage the threats of starvation and predation and the two are not mutually exclusive but occur simultaneously, with the emphasis being on the greatest immediate threat. Increased wind speed is detrimental to redshank survival because it reduces body temperature through the effects of wind chill (Evans, 1976), and they need to find sheltered habitats in these conditions. They do this by feeding in saltmarsh creeks on *Corophium*, which may also reduce their visibility to sparrowhawks and thus offer some protection from attack. Redshanks switch food prey when mud temperature falls because *Corophium* become less available in these conditions and redshank energetic requirement is increased and so redshanks cannot

meet their daily energy requirements. They then move from saltmarsh creeks onto the saltmarsh vegetation to feed on *Orchestia*, but this puts them at a greater predation risk due to them being unable to feed in the mid marsh at a safer distance from predator-concealing cover. The reason for this is that in the mid marsh, taller species of vegetation restrict foraging, probably hamper detection of an attacking sparrowhawk, and may impede escape flight take-off speed (because redshanks use escape movements of conspecifics to initiate their quick escape if they are not the first detector – see Hilton, Cresswell and Ruxton (1999). Hence, they are forced to forage in the outer marsh, where the risk of predation on the saltmarsh is at its highest (Cresswell *et al*., 2010), especially when it is cold and *Orchestia* activity decreases. In these conditions redshanks probe for *Orchestia* in the subsoil and denser vegetation with head down, which reduces their vigilance and response time to an attack (Sansom *et al*., 2009). This demonstrates that a bottom-up process is much more than a linear connection of energy flow between species, but is influenced by biotic and abiotic variables that dictate the behaviour of both predator and prey (Figure 5.1).

The results from Chapter 4 showed that redshank flocks were larger on the saltmarsh when wind speed increased in exposed areas of the estuary, increasing redshank thermoregulatory requirements, which forced them to find sheltered areas to forage. Colder mud temperatures also resulted in larger flocks on the saltmarsh because of the feeding switch from *Corophium* to *Orchestia* as detailed above. In these conditions, despite individual redshanks being less vigilant due to searching for inactive, hidden *Orchestia*, the formation of larger flocks may mitigate the threat from sparrowhawk attack owing to greater numbers of birds, being able to detect a predator more quickly, confuse a predator during escape flight, and reduce the probability of individual capture due to the dilution effect. These larger flocks may also be able to feed closer to the saltmarsh boundary in *Orchestia* rich patches and especially at creek edges, that were previously off-limits due to these areas having a higher predation risk. Higher temperatures (although perhaps more accurately less cold temperatures, because at high temperatures redshanks do not feed on the saltmarsh at all) and more active *Orchestia*, probably act as an attraction to foraging redshanks and flocks again increase on the saltmarsh. Redshank step rate increases as they chase and grab *Orchestia* in these conditions, but this may cause interference competition that depresses *Orchestia* which become temporarily unavailable. Larger flocks forming at higher temperatures also suggests that redshanks should be able to feed closer to the saltmarsh boundary, but interference competition may cause birds to become more spaced which will increase the predation risk (Figure 5.1).

5.1 Prey switching by redshanks – is this a bottom-up TMI/TMII?

Switching to alternative habitats because a prey becomes unavailable is not unusual behaviour for waders (Zwarts and Wannik, 1993). The common cockle (*Cerastoderma edule*) the primary prey of oystercatchers in the Wadden Sea, became unavailable in the long term (four years) which resulted in many birds changing habitats from tidal mud flats to feed on adjacent mussel banks (Zwarts and Wannik, 1993). Crucially, if animals are likely to suffer a reduction in prey availability that might degrade their condition and put them at risk of starvation, they will often switch their feeding behaviour (*e.g*. change habitat), to one that will enable them to gain enough energy to survive (Werner and Mittelbach, 1981), but which may put them at greater risk of predation (Sinclair and Arcese, 1995; Cresswell, 2010). If *Corophium* activity on the mud surface is depressed due to increased redshank foraging

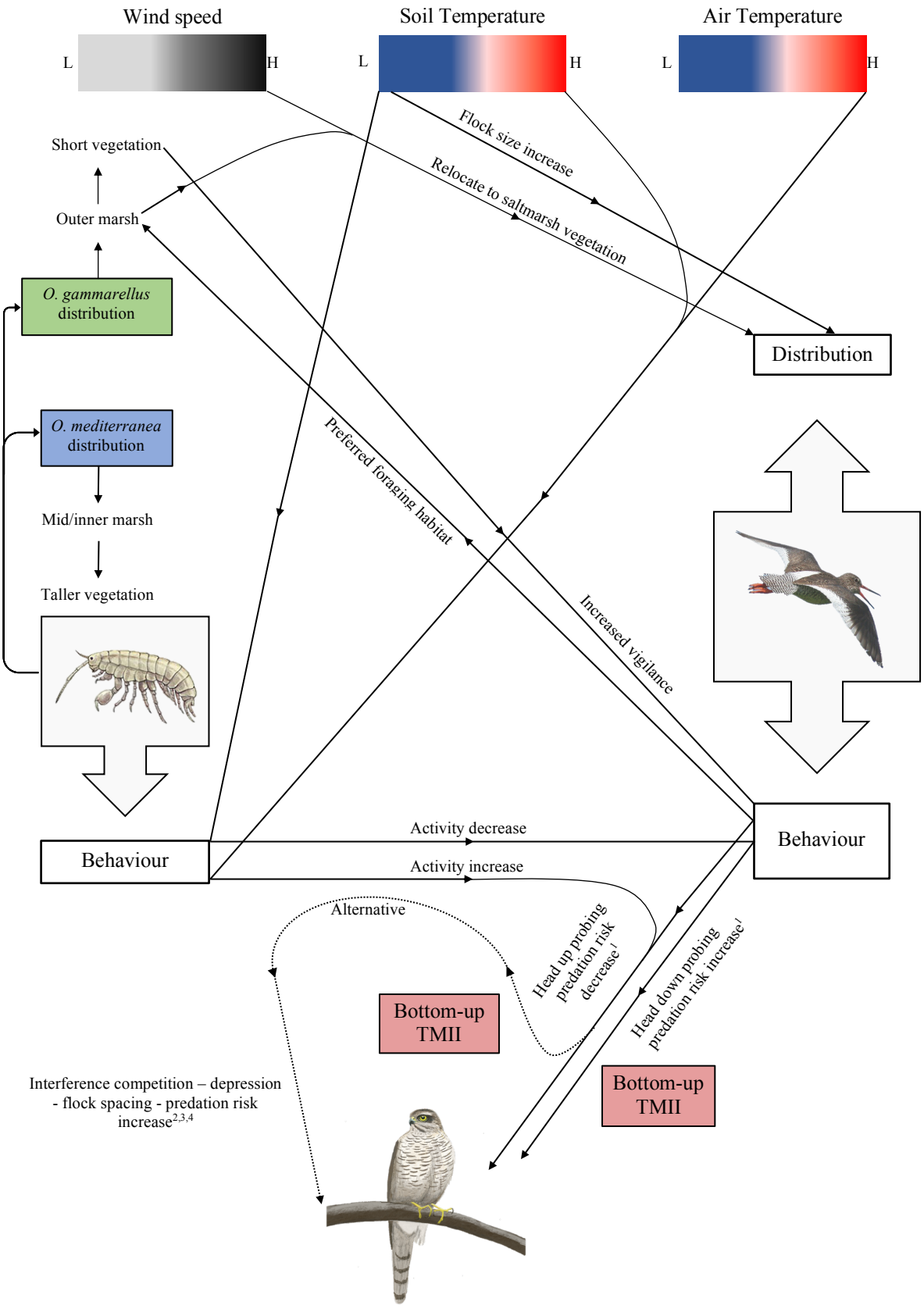


Figure 5.1 *Bottom-up effects showing the influence of wind and temperature eon distribution and behaviour of Orchestia and redshanks, and how this relates to predation risk for redshanks. References: 1. Sansom et al. (2009), 2. Krause and Ruxton (2002), 3. Minderman et al. (2006), Cresswell and Whitfield (2008).*

as suggested by Goss-Custard (1977b), which then prompts them to switch habitats and food choice to the saltmarsh, possibly increasing the predation risk from sparrowhawks, this is clearly a response to predation risk and therefore can be defined as a TMI/TMII in accordance with the definition by Luttbeg and Kirby (2005). However, it is likely that in this research the major reason for *Corophium* becoming less mobile on the surface, possibly burrowing deeper and reducing their availability to redshanks, is not caused by the predator, but by colder temperatures.

5.2 Evidence of true bottom-up trait effects

Examples of bottom-up TMIs can be observed for interactions between *Orchestia* and redshanks, redshanks and sparrowhawks and possibly TMIIs for *Orchestia* and sparrowhawks via redshanks. The behaviour of *Orchestia* can influence the behaviour of redshanks in several ways. A TMII is indicated where redshank flock size increases on the saltmarsh, due to higher temperatures and increased *Orchestia* activity. Larger flocks such as those present in winter 2 that consisted of up to 49 birds may result in interference competition between individuals which temporarily depresses *Orchesti*a availability (Minderman *et al*., 2006), so redshanks become more widely spaced (Quinn and Cresswell, 2006; Cresswell and Whitfield, 2008), and because larger flocks can also forage closer to cover, these may both increase the risk of individual birds being attacked. Therefore, the evasive actions of *Orchestia*, caused indirectly by an increase in temperature enabling larger flocks to form, negatively impacts on the feeding behaviour of redshanks, which may benefit the hunting success of sparrowhawks, producing a bottom-up TMII. Likewise, *Orchestia* are less available to redshanks at lower temperatures when they hide in denser vegetation and the subsoil. Although larger flocks form by necessity (*i.e* to reach thermoregulatory requirements due to fewer *Corophium*), to prey on *Orchestia*, their feeding technique of probing head down in these conditions, probably increases their risk of predation due to reduced vigilance. This could be mitigated because larger flocks might be more vigilant and attacks less successful due to dilution and confusion effects (Cresswell, 1994; Quinn and Cresswell, 2005). Nonetheless, this could be also viewed as a TMII where *Orchestia* behaviour critically affects some of the key determinants of attack success on redshanks (Figure 5.1).

5.3 The importance of trait effects compared to density dependent regulation

The numbers of redshanks wintering on the saltmarsh has varied over the last 28 years since Cresswell and Whitfield first investigated the predatory relationship between redshanks and sparrowhawks (Cresswell and Whitfield, 1994) (see 1.2.1, 1.3), and has probably decreased in line with total redshank counts for the Tyne estuary (includes Tyninghame saltmarsh) (Figure 5.2). During the 3 winters of this research, a general estimate of redshank numbers on the saltmarsh were 100-140, 100-120, and 40-60 (counts conducted at high spring tide, October winter 1 and December winters 2 and 3), compared to their research during winters 1989-92 which estimated 260-360, 175-379, and 180-443 birds on the saltmarsh respectively and a total of 559 kills across the three winters by sparrowhawks (111 kleptoparasited by carrion crows). This is a much greater total than shown in this research where only 11 redshank kill remains were discovered (winter 1 = 8, winter 2 = 3, winter 3 = 0. The percentage of kills to maximum redshank counts for Cresswell and Whitfield's data over the 3 winters is 32%, 50% and 57%, whereas this research shows percentages of 6%, 3% and 0%. Although the previous researchers did systematic sweeps of scrub and woodland adjacent to the saltmarsh for kill remains and this research did not, similar areas were surveyed and redshanks kills are conspicuous and persist a long time: more

kills will have occurred and been missed in this study but the recorded change in numbers is two orders of magnitude suggesting something more than survey effort is involved in discrepancy between the two sets of data.

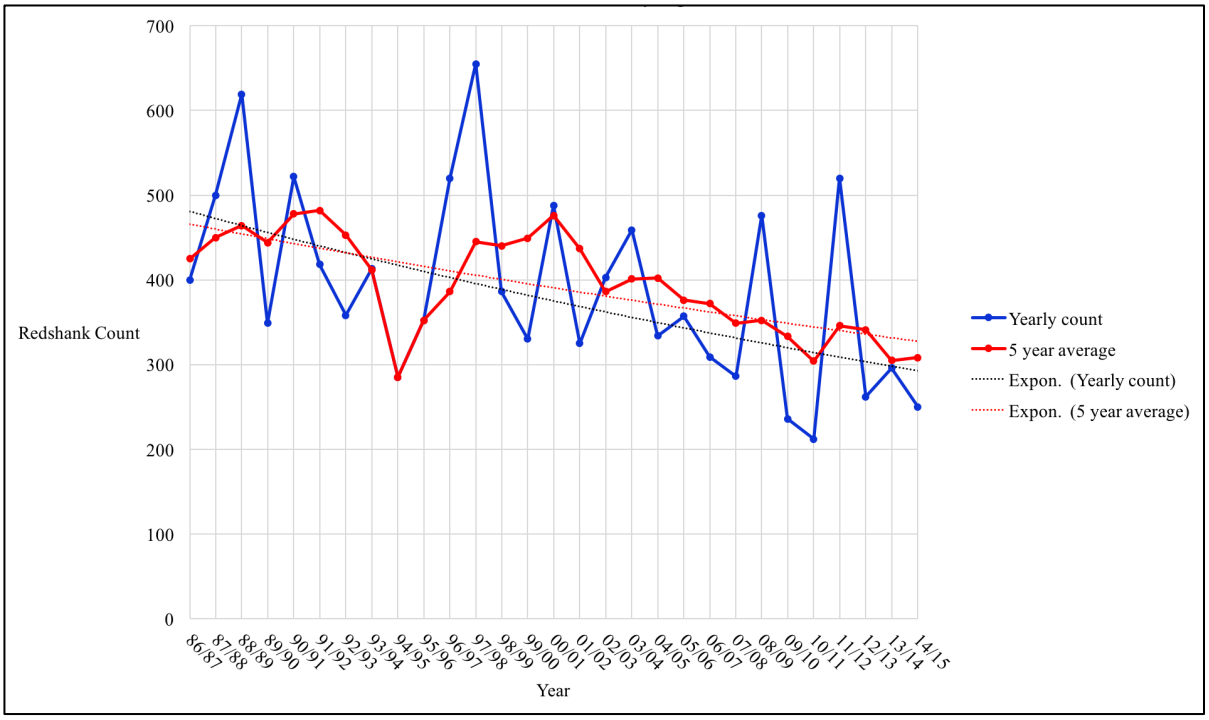


Figure 5.2 *Redshank counts Tyne estuary, Tyninghame from 1986 – 2015. Data taken from WeBS Counts, BTO (http://app.bto.org/webs-reporting/). Counts undertaken in months from Oct-April.*

Fewer overwintering redshanks probably means fewer sparrowhawks hunting on the saltmarsh and this might be evidenced by Cresswell (1994), who gave an estimation of 5 to10 regular sparrowhawks for the 3 winters of 1989-1992. Only one sparrowhawk was observed at any one time during the 3 winters of this research and on most days, none were detected. Whether fewer sparrowhawks reflects the general decline in redshank numbers at the study site is unknown. What is certain is that sparrowhawk diet usually consists of numerous species of small bird (Newton, 1986). Data from the south of Scotland (1975-76) showed that 6 bird species provided 62% of sparrowhawk diet in winter months; redwing (*Turdus iliacus*), blackbird (*T. merula*), fieldfare (*T. pilaris*), chaffinch, goldcrest (*Regulus regulus*) and woodpigeon (*Columba palumbus*). These were the only species whose contribution to the diet was more than 5%, of this woodpigeon was the most common at 34%, and 16 bird species made up 87% of the diet (Newton, 1986). Therefore, sparrowhawks appear to be adaptive with their target prey dependent on availability, so they probably take advantage of higher winter redshank populations, but can switch to other prey when this number is reduced. Notwithstanding this, sparrowhawk population trends in Scotland have fluctuated in the last 70 years (Newton, 2007). In the 1950s organo-chlorine pesticides used in agriculture were responsible for eggshell thinning (DDT) and direct deaths were associated with aldrin and dieldrin, reducing numbers (Newton, 2007). Phasing out of these chemicals saw an increase in the Scottish population until the 1980s, especially in arable areas of eastern Scotland where sparrowhawks had previously been eradicated (Newton, 2007). Subsequently, numbers have fallen due to the decline in farmland bird species and the maturing of conifer forests, that in their first years provided ideal sparrowhawk habitat (Newton, 2007). Hence, their apparent decline at the study site may not only be due to fewer winter redshanks but related to a general downward

trend in the Scottish population of sparrowhawks. What this does suggest is that when a higher population of redshanks coincides with higher numbers of sparrowhawks, these seem to have a considerable density dependent, top-down effect on the wintering redshank population. Therefore, when redshank numbers are high, sparrowhawks put greater predation effort into hunting redshanks, and although they may not be exclusive to the sparrowhawk diet, they probably reduce predation pressure on other sparrowhawk prey species. Sparrowhawks are concentrating on an abundance of prey (*i.e*. redshanks), because it is energetically more efficient to do so (Campbell *et al*., 1999), at a time in mid-winter when prey species are generally scarcer, sparrowhawk energetic needs are greater, and recent recruitment of juvenile redshanks puts pressure on the redshank population as a whole because they are competing with adults for food (Newton, 1988). Hence, more sparrowhawks may be attracted to the saltmarsh from surrounding territories because of increased redshank availability.

In these circumstances, although changes in redshank behaviour due to the sparrowhawk threat (TMI) are also evident, direct consumption has a large impact on redshank numbers. Despite evidence that trait effects can be as strong (Preisser *et al*., 2005), or larger (Creel and Christianson, 2008) than direct effects, this does not need to be the case under all conditions. In fact, the relative importance of each fluctuates across years where density dependent and then the trait effects take primacy, governed by the abundance of the sparrowhawk predator and redshank prey in the system. Therefore, it is suggested that trait effects have more influence on the sparrowhawk-redshank dynamic when numbers of both species are fewer. Although top-down DMIs and TMIs tend to overpower bottom-up effects (Schmitz, 1998), it can be seen that bottom-up effects play an important role, affecting redshank ability to balance the trade-off between starvation and predation. Moreover, density dependent and trait factors amongst sparrowhawks and redshanks exist simultaneously, varying in their magnitude between years. Nevertheless, it is suggested that top-down and bottom-up trait effects seem to be more constant than density effects, because density effects appear to be dependent on greater numbers of predators and prey, but when these are low trait effects take over as the dominant effect.

5.4 Varying trophic dynamics in the system

5.4.1 The impact of climatic variability

As the results from this study have shown, small-scale changes in temperature can influence the impact of bottom-up control in this ecosystem. Large-scale climatic variation over a greater timescale may influence the occurrence and life history of *Orchestia*, redshanks and sparrowhawks and the interactions between them Whether increases in temperature are detrimental to *Orchestia* survival is unknown, but Moore and Francis (1986) indicated that *O. gammarellus* can survive temperatures between 0°and 30°C, although Ingolfsson *et al*. (2007) found that it avoided temperatures >20°C. It is postulated by Gaston and Spicer (1998) that two separate populations (northern Scotland and south east England) had different upper thermal tolerances, that were not simply due to acclimation. The southern population had the higher tolerance, supporting the later theory of Morritt and Ingolfsson (2000) that populations of *O. gammarellus* at different latitudes have fixed genetic differences. The question is whether the Scottish populations of *Orchestia* in this study could acclimatise to a warming regime quick enough, if it produces detrimental effects for that population, because unlike some taxa such as birds and insects, they have a limited ability to migrate to escape intemperate environmental conditions. Therefore, a less hospitable habitat for

Orchestia could not only reduce their occurrence and abundance, but reduce their availability as a food source for redshanks, limiting bottom-up effects. In contrast, *Orchestia* might become more available in winter. Ingolfsson *et al*. (2007) found that Icelandic *O. gammarellus* started breeding 2-3 months earlier at thermal sites when compared to non-thermal sites, so milder winters might allow *Orchestia* to be more active throughout the winter period, thereby attracting the attention of feeding redshanks, and promoting a bottom-up effect as previously detailed.

Warmer winters are also changing the distribution of redshanks in north west Europe where the centre of their distribution moved north west during the 1980s and '90s (Maclean *et al*., 2005), which contrasts with the British Isles where their distribution has moved eastwards (Rehfisch *et al*., 2003), resulting in declines on the west coast in designated sites that were deemed of national and international importance for redshanks (Austin and Rehfisch, 2005). This contrasts with the more local data of wintering redshank numbers at the study site which appear to be declining (Figure 5.2). From a bottom-up perspective if redshank numbers at the study site are fewer, their importance as a prey resource for sparrowhawks also probably reduces. Hence, lower redshank numbers will not attract sparrowhawks and density dependent effects will be reduced and become less important, but trait effects will remain.

Being part of the land-sea interface, saltmarshes may also be impacted by climatic stochastic events, principally, sea-level rise causing inundation and storm damage which can lead to erosion (Crosby *et al*., 2016; Raposa *et al*., 2016). Nevertheless, Tyninghame is a back-barrier marsh and Sandy Hirst spit on its eastern edge may offer some protection from storms. Notwithstanding this, stochastic environmental change may be one of the greatest threats to the terrain of the marsh where considerable accretion and erosion could totally change its relief and extirpate large numbers of *Orchestia*, influencing the strength of bottom-up effects. It may be that such a change will reduce *Orchestia* numbers in the short to medium term, and sections of marsh may be destroyed or large sedimentation dumps could smother the marsh, which might then decrease *Orchestia* availability to redshanks, weakening the bottom-up effect. In this case, *Orchestia* may not be deemed a profitable prey to switch to and redshanks might forage elsewhere if *Corophium* also become less available due to saltmarsh damage. Contamination can also cause a significant impact upon saltmarshes, where a pollution event that might involve, fertiliser run-off, organic compound waste from industrial processes, and sewage waste could lead to eutrophication of surrounding seas, causing anaerobic conditions on the saltmarsh, which might alter vegetation and faunal assemblages (Packham and Willis, 1997). In addition heavy metal waste can produce acute toxicity in saltmarsh plants, and oil spills can cause medium term impacts for many species in the saltmarsh ecosystem (Packham and Willis, 1997). These changes will affect trophic dynamics and bottom-up effects, but the impacts may be complicated and the magnitude and period of damage difficult to predict.

5.4.2 The impact of stock grazing and trampling on saltmarsh *Orchestia*

Marshes grazed by domestic animals can be quite different to those that are ungrazed, with halophytic species of vegetation being reduced in grazed marshes, but which nevertheless may show increased species richness (Westhoff, 1971; Adam, 1981). Invertebrate diversity meanwhile is likely to be higher on ungrazed marshes, because a reduction in the build-up of litter and detritus on grazed marshes curbs feeding opportunities for species

including *Orchestia* (Adam, 1993). Vegetation height in ungrazed marshes in the British Isles is around 0.5 to 1m, whereas on grazed marshes this is generally a 10cm sward of dense grass (Boorman, 2003). However, the main destructive effect of grazing is due to trampling, and although sheep produce little damage except at creek-crossing paths, cattle cause heavy compaction of the soil (Adam, 1993). This then promotes waterlogging, the soil is depleted of oxygen, redox potential is reduced, and only anaerobic respiration is possible by soil bacteria; macro-invertebrates (*e.g*. *Orchestia*) find it hard to exist in these conditions (Adam, 1993). Although there is no domestic herbivore grazing at Tyninghame, a trampling problem exists in zones that run adjacent to the saltmarsh edge which are popular with walkers and have also been used by motorcycles and mountain bikes. This area is *O. gammarellus* habitat, and the sparse areas of *A. maritima* are particularly vulnerable to damage, so large mud patches form (pers. obs.). Whether, degradation by excessive compaction would be enough to have an impact on the occurrence and abundance of *Orchestia* is debatable, but a series of independent adjustments to the environment, which occur concurrently, such as long-term temperature change and/or stochastic weather incidents, might produce a negative synergistic effect on bottom-up processes and on the saltmarsh environment in general.

5.5 Evolutionary change: How will the *Orchestia*-redshank-sparrowhawk interaction co-evolve?

Animals are usually both predators and prey and each has to eat and/or prevent being eaten in order to survive (Abrams, 1986). If a prey does not adapt to outwit its predator it may be forced to exist in the less hospitable margins of its habitat or face extinction (Hoffman, 1988). Hence, the gene sets between co-evolving species of predator and prey may result in evolutionary change where an adaptation by one is aimed at overcoming or counteracting an adaptation by the other (Vermeij, 1987). This was termed the "rat race" by Rosenzweig (1973), but is now more commonly known as the "arms race" (Dawkins and Krebs, 1979). Therefore, in theory it is assumed that if a predator makes some modification to its physiology (long-term evolutionary trend), or behaviour (usually a shorter-term evolutionary trend), then its prey should make some modification to overcome it and vice versa (Abrams, 1986). The predator in an asymmetrical arms race may be disadvantaged due to what is termed the "*life-dinner*" principle, so that a successful predation event will lead to the death of the prey, but if the predator is unsuccessful, it only loses a meal and can go on to make another attempt; in this case natural selection is stronger on the prey rather than the predator (Dawkins and Krebs, 1979). Despite this, adaptive interactions between predator and prey are not clear-cut, and it is suggested that if a prey adapts to overcome predation, it is not necessarily the case that the predator will also adapt to that change (Abrams, 1986). This is because the investment that the predator makes to alter physiology or behaviour may not be profitable (*i.e*. the cost outweighs the benefit of adaptation) (Abrams, 1986). Likewise, if a predator fails to counter-adapt to an adaptation by its prey, the prey population may increase, providing more feeding opportunities for that predator (Abrams, 1986). The effect on *Orchestia*, redshank and sparrowhawk population dynamics may be complex, and as Abrams (1986) suggests, adapting behaviour and balancing trade-offs cannot be explained simply by theoretical principles.

As we have seen, feeding behaviour changes in redshanks in cold conditions when *Orchestia* become less available, which requires them to probe (head down), and makes them more vulnerable to attack by sparrowhawks. They can adapt by forming larger flocks, which increases their ability to collectively detect a predator, but according to Quinn and Cresswell (2004), sparrowhawks did not necessarily attack smaller flocks that in theory

should be more vulnerable, rather they based their attack decision on other measures of flock vulnerability (*e.g.* hours of daylight in the day, wind speed). In this example, a perceived adaptation to the predation risk by redshanks might not actually attenuate that predation risk from sparrowhawks. Sparrowhawks are still able to overcome anti-predation behaviour of redshanks (which form larger flocks), where they can target isolated and more vulnerable birds at the fringes of the flock, due to greater nearest neighbour distances. (Cresswell and Quinn, 2004; Quinn and Cresswell, 2006). Therefore, the equilibrium between predator and prey is restored and sparrowhawks and redshanks continue to co-exist. However, there are four endpoints to the arms race as described by Dawkins and Krebs (1979), where the relationship between predator and prey may result in, (1) a "*mutual local optimum*" (see Shiino *et al*., 2014; Shimizu *et al*., 2014), (2) where cyclical adaptations are continued indefinitely (see Tellier *et al*., 2014; Zaman *et al*., 2015), (3) the predator or prey may be driven to extinction (see Gibbons 1996; Rabosky and McCune, 2010), or (4) one species may reach an optimum at the expense of the other (see Gandon, 2002; Vermeij, 2014) (Dawkins and Krebs, 1979). Nonetheless, but there is no way of knowing which of these will be the result in this system

In addition, a prey species under severe predation pressure, might not need to change its behaviour to survive, but instead could move to a new habitat and conditions where it is already well adapted (Vermeij, 1987). *Orchestia* move into cracks at the edges of saltmarsh creeks and coastal redshanks could move to agricultural land and feed on soil invertebrates if the threat was adjudged to be high. Similarly, sparrowhawks being a generalist predator should not need to counter-adapt to an anti-predation adaptation from redshanks because their food source is so variable that they can switch prey type. Consequently, if predation is one of the dominant factors that controls evolution (Darwin, 1871), it is not just adaptations and counter-adaptations between predator and prey which regulate it, but a whole series of more subtle interactions, of which something as small as a behavioural response to temperature may impact across the whole system.

5.6 Making general predictions from this research

The question arising from this research is, do the findings produce results that can be applied to predict trophic dynamics in other saltmarsh systems in the British Isles, or are these results atypical in comparison? To answer this, it is first necessary to investigate environmental factors that influence saltmarsh development and compare the study site to other marshes. The back-barrier saltmarsh at Tyninghame is rare in Scotland, formed behind the shelter of sand dunes extended into a spit of land parallel to the coast (Haynes, 2016). The only other important Scottish examples of this type are: Morrich More and Dornoch Point on the Dornoch Firth; Whiteness Head, Morayshire; and Strathbeg, Aberdeenshire. The sand barrier ensures that these marshes are sheltered from stormy seas which in conjunction with high tides can produce severe erosion that can occur in other more exposed types of saltmarsh such as, open coast saltmarshes (Allen and Pye, 1992), fringing saltmarshes (*e.g.* Beauly Firth) and loch-head saltmarshes (*e.g.* Loch Sunart Head, Highland) (Haynes, 2016). In these marshes, damage caused by storms might have a catastrophic effect on *Orchestia* habitat if this is eroded and washed away. Unlike at the study site, these marshes are probably less stable and more prone to stochastic events which can change their physical appearance, and may take some time to recover. In addition, more exposed marshes hamper vegetation growth due to increased sediment accretion caused by more powerful wave action, where a dump of inorganic sediment can smother vegetation, thus reducing overall soil stability (Cousins *et al*., 2016). Accordingly, a

reduction in vegetation cover might produce an adverse effect, providing less refuge for *Orchestia* and reducing their overall abundance and distribution.

Second, one of the suggested reasons for redshanks foraging on the saltmarsh at the study site was because it offered shelter from high winds. The same could not be said for the more exposed examples of marsh, especially loch-head marshes which occur on the west and northern coasts of Scotland and are often exposed to prevailing westerly winds and storms (Haynes, 2016). These exposed marshes may not offer the same opportunity for shelter, an important consideration for foraging redshanks to reduce the effects of wind chill and maintain thermoregulatory homeostasis.

Third, not all saltmarshes are surrounded by predator concealing trees and scrub, which can provide observation posts and launch points for sparrowhawk attacks. For example, the back-barrier saltmarsh at Morrich More, Dornoch Firth has very little vegetation cover on either its north or south shores. This may restrict sparrowhawk hunting on the saltmarsh although merlin and peregrines might not be as affected, because of their different hunting strategies. If other raptor species replace sparrowhawks in these areas, then the perceived anti-predation benefits of flocking by redshanks, may not be as relevant. As an example, peregrines have been witnessed swooping to try and pick off redshanks at another estuary (Musselburgh, 20 miles to the west), where the redshanks' anti-predation strategy was to remain in situ bunched together with their heads drawn in. After the peregrine leaves they soon become dispersed and carry on foraging (pers. obs.). In this case, there is a different dynamic to flocking, where tight groupings are only formed when faced with an immediate danger, so it may be that intraspecific competition and prey depression is of little concern in this type of habitat, where peregrines are the dominant raptor and redshanks can generally forage wider apart until the predator is detected.

Fourth, the number, shape and depth of creeks between saltmarsh sites is highly variable and some have very few, whereas others like the study site, have a multitude of channel networks (Haynes, 2016). Because creeks seem to be a priority habitat for redshanks to feed on their preferred prey, *Corophium*, a saltmarsh with fewer creeks might not be ideal habitat and might not hold enough *Corophiu*m to make foraging worthwhile. Likewise, fewer creeks may reduce the opportunity for redshanks to shelter from the wind, as will shallower creeks. Moreover, the latter may not provide suitable protection from sparrowhawk attack.

Variability in the geomorphological structure of saltmarshes seems to dictate if and what species exist on them and how these species interact. It is unlikely that the trophic dynamics of each saltmarsh are the same or even similar in many respects, therefore the relationship between predators and prey will be different. One could say that the saltmarsh at Tyninghame is idiosyncratic, and it would be hard to find a saltmarsh with a trophic system that displays a similar inter-relatedness between the species, especially one that illustrates a bottom-up influence. For instance, although the abiotic effect of temperature appears to be a constant, in another saltmarsh habitat that holds fewer numbers of *Orchestia*, where creeks are scarce, or vegetation is structured differently, colder conditions and less active (hidden) *Orchestia* may not provide the alternative food source upon depletion of *Corophiu*m. Instead, redshanks may switch to alternative prey such as *Nerei*s, *Macoma*, or forage for less available *Corophium* for longer periods and at night to make up for any energetic shortfall, as suggested by Goss-

Custard (1969). Therefore, it is perhaps unwise to present the Tyninghame saltmarsh as a meaningful template for predicting trophic dynamics in other saltmarsh systems; it is an idiosyncratic system, although it might possess some similarities to other saltmarshes. Research into bottom-up effects in other saltmarsh systems would be a worthwhile topic for further study to compare and contrast with the findings of this research.

5.7 Study conclusion

To date, trophic research of relationships between species has mainly concentrated on top-down influence. One framework for understanding this is the starvation-predation risk trade-off, because the non-lethal fitness costs of behaviour to avoid predation by species can be measured in terms of reduction in foraging in the most profitable areas, where foraging is compromised below optimal levels. Bottom-up effects on trophic systems have been understudied. This is where species at a lower trophic level induce a behavioural change at a higher level, so potentially affecting the higher-level species' ability to behaviourally respond and mitigate the threat from predators.

This thesis explores the influence of bottom-up effects on the starvation-predation risk trade-off within a trophic cascade in a case study involving an *Orchestia*-redshank-sparrowhawk system on a Scottish saltmarsh, to better understand how and when bottom up effects arise. Two species of *Orchestia* were found, *Orchestia gammarellus* in a zone adjacent to the terrestrial edge, and *O. mediterranea* in the mid and inner marsh which received the most tidal coverage. *Orchestia* species prefer denser vegetation, especially on the edges of saltmarsh creeks, where position and extent is determined by each species' tolerance to saltwater coverage.

In winter, redshanks prefer to forage on the saltmarsh in muddy creeks on their preferred prey *Corophium*. Creeks also provide shelter from westerly winds and may allow redshanks to remain out of sight of sparrowhawks which hunt from trees and shrubs that skirt the saltmarsh. Nevertheless, at lower mud temperatures *Corophium* become less active and available as a food for redshanks, which results in them relocating out of saltmarsh creeks onto vegetation to feed on *Orchestia*, which are still available even in cold soil temperatures. This enables redshanks to reach their energetic requirement although it puts them at greater risk of predation, because they probe soil and denser vegetation where *Orchestia* shelter from colder temperatures, with their heads down resulting in them being less able to detect a sparrowhawk attack. This is mitigated to some extent because larger flocks form enabling greater chance of predator detection, besides causing confusion to an attacking sparrowhawk and dilution of the risk of being killed. Larger flocks may mean that redshanks are able to feed closer to the saltmarsh boundary especially in patches of *O. gammarellus* that were previously unavailable to them. Higher temperatures and more active *Orchestia* provide a stimulus to foraging redshanks which chase and grab prey items with their head up; a technique which may allow them to be more vigilant. Larger flocks again form which can result in interference competition, because when temperatures are higher, *Orchestia* will respond to predation risk by hiding (prey depression) and so birds become more widely spaced, increasing the predation risk for isolated individuals.

Therefore, in this system, temperature is a major factor that drives the starvation-predation risk trade-off because it dictates the behaviour of *Orchestia* which impacts upon redshank flock formation, feeding location, and their

ability to feed in a way that allows redshanks to detect predators. The system shows a bottom-up TMI that may develop into a bottom-up trophic cascade (TMII), where hunting sparrowhawks are indirectly affected by *Orchestia* behaviour which directly impacts upon redshank feeding behaviour. This shows that bottom-up effects work in conjunction with top-down, involving both density dependent and/or trait effects, but the magnitude of each may vary and appears to be regulated by sparrowhawk and redshank population sizes, and where these are high, density dependent predation is dominant. Whether the findings of this research can be applied to other saltmarshes is unclear, because environmental drivers shape the topography of saltmarshes and produce different species compositions and interactions between those species, making each saltmarsh distinct, so that the resultant trophic interactions are likely to be very context dependent and idiosyncratic.

CHAPTER 6. REFERENCES

Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology*, 70, pp.999–1007.

Abrams, P. A. 1982. Functional responses of optimal foragers. *The American Naturalist*, 120, pp.382–390.

Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. *The American Naturalist*, 124, pp.80–96.

Abrams, P. A. 1986. Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. *Evolution*, 40, pp.1229–1247.

Abrams, P. A. 1991. Strengths of indirect effects generated by optimal foraging. *Oikos*, 62, pp.167–176.

Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. *The American Naturalist*, 146, pp.112–134.

Abrams, P. A. 2010. Implications of flexible foraging for interspecific interactions: lessons from simple models. *Functional Ecology*, 24, pp.7–17.

Adam, P. 1981. Vegetation of British saltmarshes. *New Phytologist*, 88, pp.143–196.

Adam, P. 1993. *Saltmarsh ecology*, Cambridge: Cambridge University Press.

Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science*, 294, pp.321–326.

Alexander, M. E., J. T. A. Dick, and N. E. O' Connor. 2013. Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos*, 122, pp.1521-1531.

Allen, J. R. L., and K. Pye. 1992. Coastal saltmarshes: their nature and importance. In J. R. L. Allen and K. Pye, eds. *Saltmarshes: morphodynamics, conservation and engineering significance*. Cambridge: Cambridge University Press, pp.1–18.

Amanieu, M., and B. Salvat. 1963. *Orchestia microphthalma* description et affinites (Crustacea: Amphipoda: Talitridae). *Bulletin du Museum national d'histoire naturelle Ser 2*, 35, pp.302–310.

Anderson, B. W., R. D. Ohmart, and J. Rice. 1983. Avian and vegetation community structure and their seasonal relationships in the lower Colorado river valley. *The Condor*, 85, pp.392–405.

Anholt, B. R., and E. E. Werner. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. *Ecology*, 76, pp.2230–2234.

Arab, A., and G. M. Wimp. 2013. Plant production and alternate prey channels impact the abundance of top predators. *Oecologia*, 173, pp.331–341.

Arcas, J. 2001. Predation of common sandpiper *Actitis hypoleucos* on *Orchestia gammarellus* (Pallas 1766), (Crustacea: Amphipoda): problems in assessing its diet from pellet and dropping analysis. *Wader Study Group Bulletin*, 94, pp.31–33.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis*, 103b, pp.458–473.

Austin, G., and M. M. Rehfisch, 2005. Shifting non-breeding distributions of migratory fauna in relation to climatic change. *Global Change Biology*, pp.31–38.

Backlund, H. O. 1945. Wrack fauna of Sweden and Finland. *Opuscula Entomologica*, 5 (Supp), pp.1-236.

Baker, J. A. 1967. *The Peregrine*, London: Harper Collins.

Bakker, J. P., K. J. Nielsen, J. Alberti, F. Chan, S. Hacher, O. O. Irbarne, D. P. Kuijper, B. A. Menge, M. Schama, and R. B. Silliman, 2015. Bottom-up and top-down interactions in coastal interface systems. In T. C. Hanley and K. J. La Pierre, eds. *Trophic ecology*. Cambridge: Cambridge University Press, pp.157–200.

Barbosa, A. 1997. The effects of predation risk on scanning and flocking behaviour in dunlin. *Journal of Field Ornithology*, 68, pp.607–612.

Barton, K. 2015. MuMIN: MultiModel Inference. R package version 1.14.0.

Bates, D. M. 2010. lme4: Mixed effects modelling with R.

Bates, D., M. Mächler, M. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, pp.1–48.

Beauchamp, G. 2006. Spatial, temporal and weather factors influencing the foraging behavior of migrating semi-palmated sandpipers. *Waterbirds*, 29, pp.221–225.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences of the United States of America*, 94, pp.10735–10738.

Bell, S. S. 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecological Monographs*, 50, pp.487–505.

Bell, S. S., M. C. Watzin, and B. C. Coull. 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. *Journal of Experimental Biology and Ecology*, 35, pp.99–107.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, 18, pp.182–188.

Bergmann, C. 1847. Über die verhältnisse der wärmeökonomie der thierre zu ihrer grösse. *Göttinger Stud*, 3, pp.595-708.

Bertram, B. C. R. 1978. Living in groups: predators and prey. In J. R. Krebs and N. B. Davies, eds. *Behavioural ecology*. Oxford: Blackwell Scientific Press, pp.64-96.

Bijeleveld, A. I., E. O. Folmer, and T. Piersma. 2012. Experimental evidence for cryptic interference among socially foraging shorebirds, *Behavioral Ecology*, 23, pp.806-814.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulson, M. H. Stevens, and J-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, 24, pp.127–135.

Bolnick, D. I., and E. L. Preisser. 2005. Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. *Ecology*, 86, pp.2771–2779.

Boorman, L. 2003. *Saltmarsh Review - An overview of coastal marshes, their dynamic and sensitivity characteristics for conservation and management*, Peterborough: JNCC Report 334.

Bowlby, J. N., and J. C. Roff. 1986. Trophic structure in southern Ontario streams. *Ecology*, 67, pp.1670–1679.

Bracht, G. 1980. The jump of *Orchestia cavimana* Heller, 1865 (Crystacea, Amphipoda, Talitridae). *Experientia*, 36, pp.56–57.

Bradley, E. 1974. *The biology of Orchestia mediterranea (A. Costa) and Orchestia gammarella (Pallas) in the salt marshes of the Duddon Estuary*. Lancaster University.

Brenchley, G. A., and J. T. Carlton. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. *Biological Bulletin*, 165, pp.543–558.

Brönmark, C., and L-A. Hansson. 2007. *The biology of lakes and ponds* 2nd ed., Oxford: Oxford University Press.

Bryant, J. P., G. D. Wieland, T. Clausen, and P. Kuropat. 1985. Interactions of snowshoe hare and feltleaf willow in Alaska. *Ecology*, 66, pp.1564–1573.

Burger, J., and M. Gochfeld. 2001. Smooth-billed ani (*Crotophaga ani*) predation on butterflies in Mato Grosso, Brazil: risk decreases with increased group size. *Behavioural Ecology Sociobiology*, 49, pp.482–492.

Burt, M. D. B. 1961. A contribution to the knowledge of the cestode genus *Orphryocotyle Friis*, 1870. Zoological *Journal of the Linnean Society*, Vol XLIV, pp.645-668.

Butler, S. J., and S. Gillings. 2004. Quantifying the effects of habitat structure on prey detectability and accessibility to farmland birds. *Ibis*, 146 (Supp. 2).

Butler, S. J., M. J. Whittingham, J. L. Quinn, and W. Cresswell. 2005. Quantifying the interaction between food density and habitat structure in determining patch selection. *Animal Behaviour*, 69, pp.337–343.

Cade, T. J. 1960. Peregrine and gyrfalcon populations in Alaska. *University of California Publications in Zoology*, 63, pp.151–290.

Caldwell, G. S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. *Auk*, 103, pp.494–505.

Callaway, J. C., J. A. Nyman, and R. D. De Laune. 1996. Sediment accretion in coastal wetlands: a review and simulation model of processes. *Current Topics in Wetland Biogeochemistry*, 2, pp.2–23.

Campbell, N. A., J. B. Reece, and L. G. Mitchell. 1999. *Biology* 5th ed., Menlo Park, California: Benjamin Cummings.

Carere, C., S. Montanino, F. Moreschini, F. Zoratto, F. Chiarotti, D. Santucci, and E. Alleva. 2009. Aerial flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk. *Animal Behaviour*, 77, pp.101–107.

Carey, H. V. 1985. The use of foraging areas by yellow-bellied marmots. *Oikos*, 44, pp.273–279.

Caro, T. 2005. *Antipredator defences in birds and mammals*, Chicago: University of Chicago.

Carpenter, S. R., Kitchell, J.M. and Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. *Bioscience*, 35, pp.634–639.

Chapman, V. J. 1960. *Salt marshes and salt deserts of the world*, London: Leonard Hill Ltd.

Charmantier, G., and M. Charmantier-Daures. 2001. Ontogeny of osmoregulation in crustaceans: the embryonic phase. *American Zoologist*, 41, pp.1078–1089.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. *The American Naturalist*, 110, pp.247–259.

Childs, C. 2004. Interpolating surfaces in ArcGIS spatial analyst. *ArcUser*, July-Sept, pp.32–35.

Clarke, J. H., N. Jones, D. Hill, and G. M. Tucker. 1997. The management of set-aside within a farm and its impact on birds. In R. C. Kirkwood, ed. *The 1997 Brighton crop protection conference - weeds, Vol 3*. Brighton, UK: British Crop Protection Council, pp. 1179–1184.

van Colen, C., S. F. Thrush, S. Parkes, R. Harris, S. A. Woodin, D. S. Wethey, C. A. Pilditch, J. E. Hewitt, A. M. Lohrer, and M. Vincx. 2015. Bottom-up and top-down mechanisms indirectly mediate interactions between benthic ecosystem components. *Journal of Sea Research*, 98, pp.42-48.

Colombini, I., M. Fallaci, E. Gagnarli, Rossano. C, Scapini. F, and L. Chelazzi. 2013. The behavioural ecology of two sympatric talitrid species, *Talitrus saltator* (Montagu) and *Orchestia gammarellus* (Pallas) on a Tyrrhenian sandy beach dune system. *Estuarine, Coastal and Shelf Science*, 117, pp.37–47.

Conlan, K. E. 1991. Precopulatory mating behaviour and sexual dimorphism in the ampiphod Crustacea. In L. Watling, ed. *VIIth international colloquium on amphipoda*. Walpole: Kulwer Academic, pp. 255–282.

Cothran, R. D., K. Henderson, D. Schmidenberg, and R. A. Relyea. 2013. Phenotypically similar but ecologically distinct: differences in competitive ability and predation risk among amphipods. *Oikos*, 122, pp.1429–1440.

Cousins, L. J., M. Cousins, T. Gardiner, and G. J. C. Underwood. 2016. Factors influencing the initial establishment of salt marsh vegetation on engineered sea wall terraces in south east England. *Ocean and Coastal Management*, 143, pp.96–104.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, 53, pp.667–686.

Cowlishaw, G., M. J. Lawes, M. Lightbody, A. Martin, R. Pettifor, and J. M. Rowcliffe. 2004. A simple rule for the costs of vigilance: empirical evidence from a social forager. *Proceedings of the Royal Society London, Series B-Biological Sciences*, 271, pp.27–33.

Cramp, S., and K. E. L. Simmons. 1983. *Handbook of the birds of Europe the Middle East and North Africa - the birds of the western palearctic - waders to gulls vol III*: Oxford, Oxford University Press.

Creach, V., M. T. Schrike, G. Bertru, and A. Mariotti. 1997. Stable isotopes and gut analyses to determine feeding relationships in saltmarsh macroconsumers. *Estuarine Coastal and Shelf Science*, 44, pp.599–611.

Creel, S., and N. Creel. 1996. Limitation of African wild dogs by competition limitation with larger carinivores. *Conservation Biology*, 10, pp.526-538.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects, 23, pp.194–201.

Cresswell, W. 1993. Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Animal Behaviour*, 138, pp.684–692.

Cresswell, W. 1994a. Age-dependent choice of redshank (*Tringa totanus*) feeding location: profitability or risk? *The Journal of Animal Ecology*, 63, pp.589–600.

Cresswell, W. 1994b. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour*, 47, pp.433–442.

Cresswell, W. 1996. Surprise as a winter hunting strategy in sparrowhawks *Accipiter nisus*, peregrines *Falco peregrinus* and merlins *F. columbarius*. *Ibis*, 138, pp.684–692.

Cresswell, W. 2008. Non-lethal effects of predation in birds. *Ibis*, 150, pp.3–17.

Cresswell, W. 2010. Empirical studies of predator and prey behaviour. In M. D. Breed and J. Moore, eds. *The Encyclopaedia of Animal Behaviour*. Edinburgh: Elsevier Academic Press, pp.633–638.

Cresswell, W., J. Lind, and J. L. Quinn. 2010. Predator-hunting success and prey vulnerability: quantifying the spatial scale over which lethal and non-lethal effects of predation occur. *J Anim Ecol*, 79, pp.556–562.

Cresswell, W., and J. L. Quinn. 2004. Faced with a choice, sparrowhawks more often attack the more vulnerable prey group. *Oikos*, 104, pp.71–76.

Cresswell, W., and J. L. Quinn. 2011. Predicting the optimal prey group size from predator hunting behaviour. *Journal of Animal Ecology*, 80, pp.310–319.

Cresswell, W., J. L. Quinn, and M. J. Whittingham. 2003. Good foragers can also be good at detecting predators. *Proceedings of the Royal Society London, Series B-Biological Sciences*, 270, pp.1069–1076.

Cresswell, W., and D. P. Whitfield. 1994. The effects of raptor predation on wintering wader populations at the Tyninghame estuary, southeast Scotland. *Ibis*, 136, pp.223–232.

Cresswell, W., and D. P. Whitfield. 2008. How starvation risk in redshanks *Tringa totanus* results in predation mortality from sparrowhawks *Accipiter nisus*. *Ibis*, 150, pp.209–218.

Crosby, S. C., D. Sax, M. Palmer, H. S. Booth, L. A. Deegan, M. D. Bertness, and H. M. Leslie. 2016. Salt marsh persistence is threatened by predicted sea-level rise. *Estaurine, Coastal and Shelf Science*, 181, pp.93–99.

Crowder, L. B., D. D. Squires, and J. A. Rice. 1997. Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. *Ecology*, 78, pp.1796–1804.

Crowl, T. A., and A. P. Covich. 1990. Predator-induced life history shifts in a freshwater snail. *Science*, 247, pp.920–929.

Dahl, E. 1946. The amphipoda of the Sound - part 1 - terrestrial amphipoda. *Acta Universitatis Lundensis N.F. Adv (2)*, 42, pp.1–13.

Dahlgren, J., L. Oksanen, T. Oksanen, J. Olofsson, P. A. Hambäck, and Å. Lindgren. 2009. Plant defences to no avail? Responses of plants of varying edibility to food web manipulations in a low arctic scrubland. *Evolutionary Ecology Research*, 11, pp.1189-1203.

Daiber, F. C. 1977. Salt marsh animals: distributions related to tidal flooding, salinity and vegetation. In V. J. Chapman, ed. *Wet coastal ecosystems*. Amsterdam: Elsevier, pp. 79–108.

Darwin, C. 1871. *The origin of species*, London: Murray.

Davidson, N. C. 1981. Survival of waders during severe weather: the role of nutritional reserves. In N. V. Jones, and W. J. Wolf, eds. *Feeding and Survival Strategies of Estuarine Organisms*. London: Plenum Publishing, pp.86-102.

Davidson, N. C., and P. R. Evans. 1982. Mortality of redshank and oystercatchers from starvation during severe weather. *Bird Study*, 29, pp.183–188.

Davis, L. V., and I. E. Gray. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. *Ecological Monographs*, 36, pp.275–295.

Dawkins, R., and J. R. Krebs.1979. Arms races between and within species. *Proceedings of the Royal Society London, Series B-Biological Sciences*, 205, pp.489–511.

Dawson, W. R., C. Carey, and T. J. van't Hof. 1992. Metabolic aspects of shivering thermogenisis in passerines during winter. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, 23, pp.381–387.

Day, J. W., J. Rybczyk, J. Scarton, F. Rismondo, A. Are, D. Cecconi, and G. Cecconi. 1999. Soil accretionary dynamics, sea-level rise and the survival of wetlands in Venice lagoon: a field and modelling approach. *Estuarine Coastal Shelf Science*, 49, pp.607–628.

De Angelis, D. L. 1992. *Dynamics of nutrient cycling and food webs*, London: Chapman and Hall.

De Mars, C., G. A. Breed, J. Potts, R. Serrouya, and S. Boutin. 2016. Behaviourally-mediated interactions of landscape pattern shape predator-prey dynamics in highly altered landscapes. In *Predator-prey dynamics: from theory to management*. Revelstoke, BC, Canada, 5 Apr 2016.

Dementiev, G. P., and N. A. Gladkov. 1951. *Birds of the Soviet Union*, Jerusalem: Israel Programme for Scientific Translation.

Den Hartog, C. 1963. The amphipods of the deltaic region of the rivers Rhine, Meuse and Scheldt in relation to the hydrography of the area part II. The Talitridae. *Netherlands Journal of Sea Research*, 2, pp.40–67.

Denno, R. F. 1977. Comparison of the assemblages of sap-feeding insects (Homoptera-Hemiptera) inhabiting two structurally different salt marsh grasses in the genus Spartina. *Environmental Entomology*, pp.359–372.

Denno, R. F., and G. K. Roderick. 1992. Density-dispersal of planthoppers: effects of interspecific crowding. *Ecology*, 73, pp.1323–1334.

De Reuter, P. C., A-M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269, pp.1257–1260.

Devereux, C. L., C. McKeever, T. Benton, and M. J. Whittingham. 2004. The effect of sward height and drainage on common starlings *Sturnus vulgaris*. *Ibis*, 146 (Supp. 2).

De Vlaming, V., and V. W. Proctor. 1968. Dispersal of aquatic organisms - viability of seeds recovered from droppings of captive killdeer and mallard ducks. *American Journal of Botany*, 55, pp.20–26.

Dias, N., and M. Sprung. 2004. Population dynamics and reproduction of the amphipod *Orchestia gammarellus* (Talitridae) in a Ria Formosa saltmarsh (southern Portugal). *Crustaceana*, 76, pp.1123–1141.

Dias, P. D., J. P. Granadeiro, and J. M. Palmeirim. 2009. Searching behaviour of foraging waders: does feeding success influence their walking? *Animal Behaviour*, 77, pp.1203–1209.

Dill, L. M. 1990. Distance-to-cover and the escape decisions of an African cichlid fish *Melanochromis chipokae*. *Environmental Biology of Fishes*, 27, pp.147–152.

Dinning, B., H. De Butts, A, Marshall, and A. Spittel. 2003. Sexul selection in freshwater amphipods (*Gammarus minus*). *Journal of Ecological Research*, 5, pp.7–10.

Dobson, S. I., and J. E. Havel. 1988. Indirect prey effects: some morphological and life history responses of *Daphnia pulex* exposed to *Notonecta undulata*. *Limnology and Oceanography*, 33, pp.1274–1285.

Dolby, A. S., and T. C. Grubb Jr. 1999. Effects of winter weather on horizontal and vertical use of isolated forest fragments by bar-foraging birds. *The Condor*, 101, pp.408–412.

Dorsmann, B. A. 1935. *Notes on the life history of Orchestia bottae Milne Edwards*. University of Leiden.

Drake, B. G. 1989. Photosynthesis of salt marsh species. *Aquatic Botany*, 34, pp.167–180.

Drummond, D. C. 1960. The food of *Rattus norvegicus* (Berk), in an area of sea wall, salt marsh and mudflat. *Journal of Animal Ecology*, 29, pp.341–347.

Dugan, P. J., P. Evans, L. Goodyer, and N. C. Davidson. 1981. Winter fat reserves in shorebirds: disturbance of regulated levels by severe weather conditions. *Ibis*, 123, pp.359–363.

Dugan, J. E., D. Hubbard, M. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine, Coastal Shelf Science*, 58(Supp), pp.25–40.

Dukas, R., and A. C. Kamil. 2001. Limited attention: the constraint underlying search image. *Behavioral Ecology*, 12, pp.192-199.

Dunning Jr, J. B. 1992. *Handbook of Avian Body Masses* 2nd ed., Boca Raton: CRC Press.

Egger, M. 1979. Varied thrushes feeding on talitrid amphipods. *Auk*, 96, pp.805–806.

Eklov, P., and T. van Kooten. 2001. Facilitation among piscivorous predators: effects of prey habitat use. *Ecology*, 82, pp.2486–2494.

Ekman, J. 1987. Exposure and time use in willow tit flocks: the cost of subordination. *Animal Behaviour*, 35, pp.445–452.

Elgar, M. A. 1989. Predator vigilance and groupsize in mammals and birds: a critical review of the evidence. *Biological Review*, 64, pp.13–33.

Elgar, M. A., and C. P. Catterall. 1981. Flocking and predator surveillance in house sparrows: test of an hypothesis. *Animal Behaviour*, 29, pp.868–872.

Elkaïm, B., J. P. Irlinger, and S. Pichard. 1985. Dynamiqu de la population d'*Orchestia mediterranea* L. (Crustace, Amphipode) dans l'estuaire du Bou Regreg (Maroc). *Canadian Journal of Zoology*, 63, pp.2800–2809.

Elliott, M., M. G. O'Reilly, and C. J. L. Taylor. 1990. The Forth estuary: a nursery and overwintering area for North Sea fishes. *Hydrobiologica*, 195, pp.89–103.

Ellrich, J. A. 2010. Effects of crab predation risk on periwinkle grazing activity. MSc Thesis, University of Marburg, Germany.

Emlen, J. M. 1966. The role of time and energy in food preference. *American Naturalist*, 100, pp.611–617.

Enckell, P. H. 1980. *Kräftdjur*, Signum, Lund, Sweden.

Estrada, A., and B. Arroyo. 2012. Occurrence vs abundance models: difference between species with varying aggregation patterns. *Biological Conservation*, 152, pp.37-45.

ESRI, 2013. ArcGIS desktop: Release 10.

Evans, P. R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea*, 64, pp.117–139.

Evans, P. R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal prey. In E. Naylor and R. G. Hartnell, eds. *Cyclic phenomena in marine plants and animals*. Marine Biology Symposium, Isle of Man, 27 Sept 1978.

Evans, M. E., N. Villar, N. A. Littlewood, R. J. Pakeman, S. E. Evans, P. Dennis, J. Skartveit, and S. M. Redpath. 2015. The cascading impacts of livestock grazing in upland ecosystems: a 10-year experiment. *Ecosphere*, 6, pp.1-15.

Fish, J. D., and A. Mills. 1979. The reproductive biology of *Corophium volutator* and *C. arenarium* (Crustacea: Amphipoda). *Journal of the Marine Biological Association*, 59, pp.355–368.

Foster, W. A., and J. E. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293, pp.466–467.

Frederiksen, M., M. Edwards, A. Richardson, N. C. Halliday, and S. Wanless. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J Anim Ecol*, 75, pp.1259–1268.

Freeman, A. 2017. Size-dependent trait-mediated indirect interactions among sea urchin herbivores. *Behavioral Ecology*, 17, pp.182-187.

Freeman, E. A., and G. Moisen. 2008. Presence/absence: an R package for presence/absence analysis. *Journal of Statistical Software*, 23, pp.1–31.

Fretwell, S. D. 1977. The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine*, 20, pp.169–185.

Fridley, J. 2010. Generalised additive models in R., 2016 (14 July 2016). Available at: http://plantecology.syr.edu/fridley/bio793/gam.html [Accessed 30 March 2017].

Friend, J. A., and M. Richardson.1986. Biology of terrestrial amphipods *Arcitalitrus dorrieni* in Britain and Ireland: watch this space. *Isopoda*, 2, pp.7–11.

Furnell, J., and S. L. Hull. 2014. Cliff top habitats provide important alternative feeding resources for wading birds of conservation importance wintering on non-estuarine coasts. *Estuarine and Coastal Shelf Science*, 139, pp.119–126.

Gallagher, A. J., S. Creel, R. P. Wilson, and S. J. Cooke. 2017. Energy landscapes and the landscape of fear. *Trends in Ecology and Evolution*, 32, pp.88-96.

Gandon, S. 2002. Local adaptation and the geometry of host-parasite coevolution. *Ecology Letters*, 5, pp.246-256.

Gaston, K. J., and J. I. Spicer. 1998. Do upper thermal tolerances differ in geographically separated populations of the beachflea *Orchestia gammarellus* (Crustacea: Amphipoda)? 229, pp.265–276.

Gendron, R. P., and J. E. T. Staddon. 1983. Searching for cryptic prey: the effect of search rate. *The American Naturalist*, 121, pp.172–186.

Gerritsen, A. F. C., and A. Meiboom. 1986. The role of touch in prey density estimation by *Calidris alba*. *Netherlands Journal of Zoology*, 36, pp.530–562.

Gessaman, J. A. 1973. *The ecological energetics of homeotherms*, Logan: Utah State University Press.

Gibbons, A. 1996. Did neanderthals lose the evolutionary "arms" race? *Science*, 272, pp.1586-1587.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology*, 68, pp.1856–1862.

Ginsburger-Vogel, T., and H. Charniaux-Cotton. 1982. Sex determination. In D. E. Bliss and L. G. Abele, eds. *The biology of Crustacea, Vol 2, embriology, morphology and genetics*. New York: Academic Press, pp. 257–281.

Glazier, D. S. 1999. Freshwater springs: classifying the diversity of life. Available at: http://legacy.juniata.edu/departments/biology/eco/documents/Dinning_etal.pdf [Accessed February 16, 2013].

Glutz Von Blotzheim, U. N., K. M. Bauer, and E. Bezzei. 1971. *Handbuch der vogel mitteleuropas* 4th ed., Frankfurt: Akademische Verlagsgesellschaft.

Goodhart, C. B. 1941. The ecology of amphipoda in a small estuary in Hampshire. *Journal of Animal Ecology*, 10, pp.306–322.

Goslee, S. C., and D. L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological software. *Journal of Statistical Software*, 22, pp.1-19.

Goss-Custard, J. D. 1966. *The feeding ecology of the Redshank,* (*Tringa totanus* (L.)) *in winter on the Ythan Estuary, Aberdeenshire.* Unpublished Ph.D Thesis, University of Aberdeen.

Goss-custard, J. D. 1967. The winter predation of *Corophium volutator* by redshank. *Ibis*, 109, p.475.

Goss-Custard, J. D. 1969. The winter feeding ecology of the redshank *Tringa totanus*. *Ibis*, 111, pp.338–356.

Goss-Custard, J. D. 1970a. The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *Journal of Animal Ecology*, 39, pp.91–113.

Goss-Custard, J. D. 1970b. Feeding dispersion in some overwintering wading birds. In J. H. Crook, ed. *Social behaviour in birds and mammals.* New York: Academic Press, pp.3-35.

Goss-Custard, J. D. 1975. Beach feast. *Birds*, (Sept/Oct), pp.23–26.

Goss-Custard, J. D. 1976. Variation in the dispersion of redshank (*Tringa totanus*) on their winter feeding grounds. *Ibis*, 118, pp.257–263.

Goss-Custard, J. D. 1977a. Optimal foraging and the size selection of worms by redshank (*Tringa totanus*) in the field. *Animal Behaviour*, 25, pp.10–29.

Goss-Custard, J. D. 1977b. Predator responses and prey mortality in redshank, *Tringa totanus* (L.), and a preferred prey, *Corophium volutator* (Pallas). *Journal of Animal Ecology*, 46, pp.21–35.

Goss-Custard, J. D. 1977c. The energetics of prey selection by redshank, *Tringa totanus* (L.), in relation to prey density. *Journal of Animal Ecology*, 46, pp.1–19.

Goss-Custard, J. D. 1980. Competition for food and interference among waders. *Ardea*, 68, pp.31–52.

Goss-Custard, J. D., and R. E. Jones. 1976. The diets of redshank and curlew. *Bird Study*, 23, pp.233–243.

Goss-Custard, J. D., S. E. A. leV. dit Durell. 1987. Age related effects in oystercatchers *Haemotopus ostralegus*, feeding on mussells *Mytilus edulis*. 1. Foraging efficiency and interference. *Journal of Animal Ecology*, 56, pp.521-536.

Goss-Custard, J. D., R. M. Warwick, R. McGrorty, R. T. Clarke, B. Pearson, W. E. Rispin, S. E. A. Le V. Dit Durell, and R. J. Rose. 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. *Journal of Applied Ecology*, 28, pp.1004–1026.

Gourley, S. A., and Y. J. Lou. 2014. A mathematical model for the spatial spread and biocontrol of the Asian longhorned beetle. *SIAM Journal of Applied Mathematics*, 74, pp.864-884.

Grand, T. C., and L. M. Dill. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behavioral Ecology*, 8, pp.437–447.

Graven, S. A., and S. G. Morgan. 2016. Prey state alters trait-mediated indirect interactions in rocky tidal pools. *Functional Ecology*, 30, pp.1574-1582.

Gray, R. D., and M. Kennedy. 1994. Perceptual constraints on optimal foraging: a reason for departures from the ideal free distribution. *Animal Behaviour*, 47, pp.469–471.

Griswold, M.W., and L. P. Lounibos. 2006. Predator identity and additive effects in a treehole community. *Ecology*, 87, pp.987–995.

Haahr, M. 2013. Random.org - True random number service. Available at: https://www.random.org [Accessed November 11, 2013].

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *The American Naturalist*, 94, pp.421–425.

Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of theoretical Biology*, 31, pp.295–311.

Harris, G. J., and E. Morgan. 1986. Seasonal and semi-lunar modulation of the endogenous swimming rhythmn in the estuarine amphipod *Corophium volutator* (Pallas). *Marine Behaviour and Physiology*, 12, pp.303–314.

Harris, J. T., and D. M. Clement. 1975. Greenland peregrines at their eyries: a behavioral study of the peregrine falcon. *Meddelelser Om Grønland*, 205, pp.1–28.

Hass, C. D., and D. Valenzuela. 2002. Anit-predator benefits of group living in white-nosed coatis (*Nasua narica*). *Behavioural Ecology Sociobiology*, 51, pp.570–578.

Haynes, T. A. 2016. *Commissioned Report No. 786 - Scottish saltmarsh survey national report*, Inverness, Scottish National Heritage.

Hayward, P. J., and J. S. Ryland. 1990. The marine fauna of the British Isles - Volume 1 - Introduction and protozoans to arthropods.

Heads, P. A. 1986. The costs of reduced feeding due to predator avoidance: potential effects on growth and fitness in *Ischnura elegans* larvae (Odonata: Zygoptera). *Ecological Entomology*, 11, pp.369-377.

Heithus, M. R., and L. M. Dill. 2002. Food availability and tider shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, pp.480–491.

Henzler, C. M., and A. Ingolfsson. 2007. The biogeography of the beachflea, *Orchestia gammarellus* (Crustacea, Amphipoda, Talitridae), in the North Atlantic with special reference to Iceland: a morphometric and genetic study. *Zoologica Scripta*, 37, pp.57–70.

Hik, D. S. 1995. Does risk of predation influence population dynamics? Evidence from the cyclic decline of snowshoe hares. *Wildlife Research*, 22, pp.115–129.

Hilton, G. M., W. Cresswell, and G. D. Ruxton. 1999. Intraflock variation in the speed of escape-flight response on attack by an avian predator. *Behavioral Ecology*, 10, pp.391–395.

Hilton, G. M., G. D. Ruxton, and W. Cresswell. 1999. Choice of foraging area with respect to predation risk in redshanks: the effects of weather and predator activity. *Oikos*, 87, pp.295–302.

Hoffman, A. 1988. Evolution and escalation: an ecological history of life (book review). *Journal Evolutionary Biology*, 1, pp.369–370.

Holling, C. S. 1959. The components of predation as revealed by a study of a small mammal predation of the european pine sawfly. *Canadian Entomologist*, 91, pp.293–320.

Hollis, K. L. 2017. Ants and antlions: the impact of ecology, coevolution and learning on an insect predator-prey relationship. *Behavioural Processes*, 139, pp.4-11.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology*, 67, pp.737-748

Houston, A.I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society London, Series B*, 341, pp.375–397.

van den Hout, P. J., J. A. van Gils, F. Robin, F. van der Geest, M. Dekinga, and T. Piersma. 2014. Interference from adults forces young red knots to forage for longer and in dangerous places. *Animal Behaviour*, 88, pp137-146.

Howes, B. L., R. Howarth, J. Teal, and I. Valiela. 1981. Oxydation-reduction potential in a salt marsh: spatial patterns and interaction with primary production. *Limnology and Oceanography*, 26, pp.350–360.

Howes, B. L., and D. D. Goehringer. 1994. Pore-water drainage and dissolved organic carbon and nutrient losses through the intertidal creekbanks of a New England salt marsh. *Marine Ecology Progress Series*, 114, pp.289–301.

Huang, C., and A. Sih. 1990. Experimental studies on behaviorally mediated indirect interactions through a shared predator. *Ecology*, 71, pp.1515–1522.

Huisman, J., J. P. Grover, R. van der Wal, and J. van Andel. 1999. Competition for light, plant species replacement and herbivore abundance along productivity gradients. In H. Olff, V. K. Brown, and R. H. Drent, eds. *Herbivores: between plants and predators*. London: Blackwell Science, pp. 239–269.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, 73, pp.724–732.

Hurley, D. E. 1956. Terrestrial and littoral amphipods of the genus *Orchesti*a. Family Talitridae. *Transactions of the Royal Society of New Zealand*, 84, pp.359–389.

Hurley, D. E. 1968. Transition from water to land of amphipod crustaceans. *American Zoologist*, 8, pp.327–353.

Inger, R., S. Bearhop, J. Robinson, and G. D. Ruxton. 2006. Prey choice affects the trade-off balance between predation and starvation in an avian herbivore. *Animal Behaviour*, 71, pp.1335–1341.

Ingolfsson, A. 1977. Distribution and habitat preferences of some inter tidal amphipods in Iceland. *Acta Naturalia Islandica*, 25, pp.1–28.

Ingolfsson, A., O. P. Olafsson, and D. Morris. 2007. Reproduction and life-cycle of the beachflea (*Orchestia gammarellu*s) (Pallas) (Crustacea: Amphipoda) at thermal and non-thermal sites in the intertidal of Iceland: how important is temperature? *Marine Biology - International Journal on Life in Oceans and Coastal Waters*, 150, pp.1333–1343.

Ioannou, C. C., C. R. Tosh, L. Neville, and J. Krause. 2008. The confusion effect - from neutral networks to reduced predation risk. *Behavioural Ecology*, 19, pp.126–130.

Irons, D. B., R. G. Anthony, and J. A. Estes. 1986. Foraging strategies of glaucous-winged gulls in a rocky intertidal community. *Ecology*, 67, pp.1460–1474.

Jenkins, B., R. L. Kitching, and S. L. Pimm. 1992. Productivity, disturbance, and food web structure at a local spatial scale in experimental container habitats. *Oikos*, 65, pp.249–255.

Johnston, V. R. 1942. Factors influencing local movements of woodland birds in winter. *The Wilson Bulletin*, 54, pp.192–198.

Jones, M. B., and G. D. Wigham. 1993. Reproductive biology of *Orchestia gammarellus* (Crustacea:Amphipoda) living in a sewage treatment works. *Journal of the Marine Biological Association*, 73, pp.405–416.

Jones, N. S. 1948. The ecology of the amphipoda of the south of the Isle of Man. *Journal of the Marine Biological Association*, 27, 400-439.

Kaby, U., and J. Lind. 2003. What limits predator detection in blue tits (*Cyanistes caeruleus*): posture, taks or orientation. *Behavioural Ecology Sociobiology*, 54, pp.534–538.

van de Kam, J., B. J. Ens, T. Piersma, and L. Zwarts. 2004. *Shorebirds. An illustrated behavioural ecology*, Utrecht: KNNV Publishers.

Karlbrink, F. 1969. Distribution and dispersal of Talitridae (Amphipoda) in southern Sweden. *Oikos*, 20, pp.327–334.

Kenward, R. E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology*, 47, pp.449–460.

Kneib, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries*, 7, pp.392–412.

Kneib, R. T. 1994. Spatial pattern, spatial scale, and feeding in fishes. In K. L. Fresh and R. J. Feller, eds. *Theory and application in fish feeding ecology*. Columbia: University of South Carolina.

van de Koppel, J., J. Huisman, R. van der Wal, and H. Olff. 1996. Patterns of herbivory along a productivity gradient: empirical and theoretical investigation. *Ecology*, 77, pp.736–745.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology*, 72, pp.2249–2260.

Kraeuter, J. N., and P. L. Wolf. 1974. The relationship of marine macroinvertebrates to salt marsh plants. In R. J. Reimold and W. H. Queen, eds. *Ecology of Halophytes*. New York: Academic Press, pp. 449–462.

Krause, J., and G. D. Ruxton. 2002. *Living in Groups*, Oxford: Oxford University Press.

Krebs, J. R., D. W. Stephens, and W. J. Sutherland. 1983. Perspectives in optimal foraging. In A. H. Brush and G. A. Clark, eds. *Perspectives in ornithology*. Cambridge: Cambridge University Press, pp. 165–215.

Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. R. 2001. What drives the 10-year cycle of snowshoe hares? *Bioscience*, 51, pp.25–36.

Křivan, V., and O. J. Schmitz. 2004. Trait and density mediated indirect interactions in simple food webs. *Oikos*, 107, pp.239-250.

Kuijper, D. P. J., and J. P. Barker. 2005. Top-down control of small herbivores on salt-marsh vegetation along a productivity gradient. *Ecology*, 86, pp.914–923.

Kuznetsova, A., P. Bruun Brockhoff, and R. Haubo Bojesen Christensen. 2016. lmerTest: Tests in linear mixed models. R package version 2.3-30. Available at: http://cran.r-project.org/package=lmerTest [Accessed March 16, 2017].

Laffaille, P., S. Brose, E. Feunteun, A. Baisez, and J-C Lefeuvre. 1998. The role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel Bay. *Hydrobiologia*, 373/374, pp.121–133.

Laffaille, P., J. Petillon, E. Parlier, L. Valery, F. Ysnel, A. Radureau, E. Feunteun, and J-C. Lefeuvre. 2005. Does the invasive plant *Elymus athericus* modify fish diet in tidal salt marshes? *Estuarine, Coastal snd Shelf Science*, 65, pp.739–746.

Lank, D. B., R. W. Butlet, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos*, 103, pp.303–319.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, 29, pp.1401-1409.

Laverack, L. S., and M. Blackler.1974. *Fauna and flora of St Andrews bay*, Edinburgh: Scottish Academic Press.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist*, 134, pp.922–949.

Leroux, S., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters*, 11, 1147-1156.

Leroux, S. J., and M. Loreau. 2015. Theoretical perspectives on bottom-up and top-down interactions across ecosystems. In T. C. Hanley and K. J. La Pierre, eds. *Trophic ecology: bottom-up and top-down interactions across aquatic and terrestial systems*. Cambridge: Cambridge University Press.

Li, M., Y. Li, Q. Lei, and Z. Yang. 2009. Biocontrol of Asian longhorned beetle larva by releasing eggs of *Dastarcus helophoroides* (Coleoptera: Bothrideridae). *Scientia Silvae Sinicae*, 45, pp.78-82.

Lima, S. L. 1986. Predation risk and unpredictable feeding conditions - determinants of body-mass in birds. *Ecology*, 67, pp.377–385.

Lima, S. L. 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. *Behaviour*, 102, pp.231–238.

Lima, S. L. 1988. Vigilance during the initiation of daily feeding in dark-eyed juncos. *Oikos*, 53, pp.12–16.

Lima, S. L. 1995. Back to basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, 49, pp.11–20.

Lima, S. L. 1998a. Nonlethal effects in the ecology of predator-prey interactions - what are the ecological effects of anti-predator decision-making? *Bioscience*, 48(1), pp.25–34.

Lima, S. L. 1998b. Stress and decision making under the risk of predation: recent development from behavioural, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, 27, pp.215–290.

Lima, S. L., and P. A. Bednekoff. 1999. Back to basics of anti-predatory vigilance: can nonvigilant animals detect attack. *Animal Behaviour*, 58, pp.537–543.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, pp.619–640.

Lima, S. L., and J. T. Valone. 1986. Influence of predation risk on diet selection: a simple example in the grey squirrel. *Animal Behaviour*, 34, pp.536–544.

Lima, S.L., K. L. Wiebe, and L. M. Dill. 1987. Protective cover and the use of space by finches: is closer better? *Oikos*, 50, pp.225–230.

Lin, J. 1989. Influence of location in a salt marsh on survivorship of ribbed mussels. *Marine Ecology Progress Series*, 56, pp.105–110.

Lincoln, R. J. 1979. *British Marine Amphipoda: Gammaridea*, London: British Museum (Natural History).

Lind, J., and W. Cresswell. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, 16, pp.945–956.

Lindstrom, A. 1989. Finch flock size and risk of hawk predation at a migratory stopover site. *Auk*, 106, pp.225–232.

Little, C. 2000. *The Biology of soft shores and estuaries*, Oxford: Oxford University Press.

Liu, R. S., and S. A. Gourley. 2014. A model for the biocontrol of mosquitos using predatory fish. *Discrete and Continuous Dynamical Systems - Series B*, 19, pp.3283-3298.

Logan, J. D., and W. Wolesensky. 2007. Accounting for temperature in predator functional responses. *Natural Resource Modelling*, 20, pp.549–574.

Logan, J. D., W. Wolesensky, and A. Joern. 2006. Temperature-dependent phenology and predation in arthropod systems. *Ecological Modelling*, 196, pp.471–482.

Lourenço, P. M., T. Catry, and J. P. Granadeiro. 2017. Diet and feeding ecology of the wintering shorebird assemblage in the Bijagós archipelago, Guinea-Bissau. *Journal of Sea Research*, 128, pp.52-60.

Losey, J. E., and R. F. Denno. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, pp.2143–2152.

Lubchenko, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *The American Naturalist*, 112, pp.23–39.

Ludwig, D., and L. Rowe.1990. Life history strategies for energy gain and predator avoidance under time constraints. *The American Naturalist*, 135, pp.686–707.

Luttbeg, B., and J. L. Kirby. 2005. Are scared prey as good as dead? *Trends in Ecology and Evolution*, 20, pp.416–418.

Lyly, M. S., A. Villers, E. Koivisto, P. Helle, T. Ollila, and E. Korpimäki. 2015. *Trends in Ecology and Evolution*, 5, pp.503-514.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist*, 100, pp.603–609.

Maclean, I. M. D., G. E. Austin, H. Mellan, and T. Girling. 2005. *Wetland bird survey alerts 2003/2004: changes in numbers of wintering waterbirds in the constituent countries of the United Kingdom, special protection areas (SPAs) and sites of special scientific interest (SSSIs)*. Research Report No 416, Thetford.

Magnhagen, C. 1988. Predation risk and foraging in juvenile pink (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*). *Canadian Journal of Fisheries and Aquatic Sciences*, 45, pp.592–596.

Mangel, M., and C. W. Clark. 1986. Toward a unified foraging theory. *Ecology*, 67, pp.1127–1138.

van Mannen, W. 2001. Influence of weather circumstances on behaviour and hunting success of wintering long-eared owls *Asio otus*. *Limosa*, 74, pp.81–86.

Mantzouki, E., F. Yesnel, A. Carpentier, and J. Pétillon. 2012. Accuracy of pitfall traps for monitoring populations of the amphipod *Orchestia gammarellus* (Pallas 1766) in saltmarshes. *Estuarine, Coastal and Shelf Science*, 113, pp.314–316.

Masman, D., M. Gordijn, S. Daan, and C. Dijkstra. 1986. Ecological energetics of the kestrel - field estimates of energy intake throughout the year. *Ardea*, 74, pp.24–39.

Mateo, R., R. Guitart, and A. J. Green. 2000. Determinants of lead shot, rice, and grit ingestion in ducks and coots. *Journal of Woldlife Management*, 64, pp.939–947.

Materassi, M., G. Innocento, D. Berzi and S. Focardi. 2017. Kleptoparisitism and complexity in a multi-trophic web. *Ecological Complexity*, 29, pp.49-60.

Matsuda, H., P. A. Abrams, and H. Horis. 1993. The effect of adaptive antipredator behavior on exploitative competition and mutualism between predators. *Oikos*, 68, pp.549–559.

McNamara, A. I., and J. M. Houston. 1987. Starvation and predation as factors limiting population size. *Ecology*, 68, pp.1515–1519.

Meadows, P. S., and A. A. Ruagh. 1981. Temperature preferences and activity of *Corophium volutator* (Pallas) in a new choice apparatus. *Sarsia*, 1, pp.67-72.

Meaney, R. A., I. Valiela, and J. M. Teal. 1976. Growth, abundance and distribution of larval tabanids in experimentally fertilized plots on a Massachusetts saltmarsh. *Journal of Applied Ecology*, 13, pp.323–332.

Mech, L. D., D. W. Smith, K. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management*, 65, pp.998–1003.

Meents, J. K., B. W. Anderson, and R. D. Ohmar. 1982. Vegetation relationships and food of sage sparrows wintering in honey mesquite habitat. *Wilson Bulletin*, 94, pp.129–138.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*, 65, pp.21–74.

Menge, B. A., E. L. Berlow, C. J. Blanchette, S. A. Navarette, and S. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs*, 64, pp.249–286.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutierrez. 2003. Thirteen years of shifting top-down and bottom-up control. *Bioscience*, 53, pp.633–646.

Milne, A. 1961. Definition of competition among animals. *Symposia of the Scoiety for Experimental Biology*, 15, pp.40–71.

Minderman, J., J. Lind, and W. Cresswell. 2006. Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology*, 75, pp.713–723.

Mitchell, P. I., I. Scott, and P. R. Evans. 2000. Vulnerability to severe weather and regulation of body mass of Icelandic and British redshank *Tringa totanus*. *Journal of Avian Biology*, 31, pp.511–521.

Mittelbach, G. G., 1988. Competition among refuging sunfishes and effects of fish density on littoral zone invertebrates. *Ecology*, 69, pp.614–623.

Moore, J. 2004. Detritus, trophic dynamics and biodiversity. *Ecology Letters*, 7, pp.584-600.

Moore, P. G., and C. H. Francis. 1985. Some observations on food and feeding of the supralittoral beach-hopper *Orchestia gammarellus* (pallas) (Crustacea, Amphipoda). *Ophelia*, 24, pp.183–197.

Moore, P. G., and C. H. Francis. 1986a. Environmental tolerances of beach-hopper *Orchestia gammarellus* (Pallas) (Crustacea, Amphipoda). *Marine Environmental Research*, 19, pp.115–129.

Moore, P. G., and C. H. Francis. 1986b. Notes on breeding periodicity and sex ratio of *Orchestia gammarellus* (Pallas) (Crustacea: Amphipoda) at Millport, Scotland. *Journal of Experimental Marine Biology and Ecology*, 95, pp.203–209.

Morgan, E. 1965. The activity rhythm of the amphipod *Corophium volutator* (Pallas) and its possible relationship to changes in hydrostatic pressure associated with the tides. *Journal of the British Ecological Society*, 34, pp.731–746.

Morris, J. M. 2005. *Firth of Forth National Vegetation Classification Survey 2003*, Scottish Natural Heritage Commissioned Report No 92 (ROAME No F03LH16).

Morris, R. J. 2008. Community ecology: how green is the Arctic tundra? *Current Biology*, 18, pp.256–258.

Morritt, D., and A. Ingolfsson. 2000. Upper thermal tolerances of the beachflea *Orchestia gammarellus* (Pallas) (Crustacea: Amphipoda: Talitridae) associated with hot springs in Iceland, 255, pp.215–227.

Morritt, D., and J. I. Spicer. 1998. The physiological ecology of talitrid amphipods: an update. *Canadian Journal of Zoology*, 76, pp.1965–1982.

Morritt, D., and D. I. Stevenson. 1993. Factors influencing breeding initiation in the beach flea *Orchestia gammarellus* (Pallas) (Crustacea: Amphipoda). *Journal of Experimental Marine Biology and Ecology*, 165, pp.191–208.

Mowles, S. L., S. D. Rundle, and P. A. Cotton. 2011. Susceptibility to predation affects trait-mediated indirect interactions by reversing interspecific competition. *PLoS ONE*, 6. Published online July 17, 2011. https://doi.org/10.1371/journal.pone.0023068.

Neill, S. R. S. J., and J. M. Cullen. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopods and fish predators. *Journal of Zoology*, 172, pp.549–569.

Newton, I. 1986. *The sparrowhawk*, London: Poyser.

Newton, I. 1988. A key factor analysis of a sparrowhawk population. *Oecologia*, 76, pp.588–596.

Newton, I., 2007. Sparrowhawk (*Accipiter nisus*). In R. Forrester *et al*., eds. *The birds of Scotland - volume 1*. Aberlady, East Lothian: The Scottish Ornithologists' Club.

Nilsson, P.A., and G. D. Ruxton. 2004. Temporally fluctuating prey and interfering predators: a positive feedback. *Animal Behaviour*, 68, pp.159–165.

O'Reilly, M.G. 2011. *Scottish invertebrate species knowledge dossier: amphipoda (marine and freshwater shrimps, whale-lice, terrestrial shrimps and sandhoppers)*, Edinburgh: Buglife - Invertebrate Conservation Trust.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, 118, pp.240–261.

Oksanen, T., M. E. Power, and L. Oksanen. 1995. Ideal free habitat selection and consumer-resource dynamics. *The American Naturalist*, 146, pp.565–585.

Oksanen, L., and T. Oksanen. 2000. The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist*, 155, pp.703–723.

Olff, H., J. De Leeuw, J. P. Bakker, R. J. Platerink, H. J. van Wijnen, and W. De Munck. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *Journal of Ecology*, 85, pp.799–814.

OS 1:25; 000 Scale Raster, 2016. [WMS web map service]. *25k Coverage: nt67 and nt68*.

OS MasterMap Topography Layer, 2011. [GML geospatial data]. *Coverage: Scotland*.

Owen, J. H. 1932. The feeding habits of the sparrowhawk. *British Birds*, 25, pp.151–155.

Packham, J. R., and M. J. Liddle. 1970. The Cefni salt marsh, Anglesey and its recent development. *Field Studies*, 3, pp.331–356.

Packham, J. R. and A. J. Willis. 1997. *Ecology of dunes, salt marsh and shingle*, London: Chapman and Hall.

Paine, R. T. 1992. Food-web analysis through field measurements of per capita interaction strength. *Nature*, 355, pp.73–75.

Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology*, 49, pp.667–685.

Partridge, L., and P. Green. 1985. Intraspecific feeding specialisations and population dynamics. In R. M. Sibly and R. H. Smith, eds. *Behavioural ecology: ecological consequences of adaptive behaviour*. Oxford: Blackwell Scientific Press, pp. 207–226.

Paulluault, M. 1954. Notes ecologiques sur le *Talitrus saltator*. *Archives de zoologie experimentale et generale*, 91, pp.105–129.

Pavesi, L., and E. De Mathaeis. 2013. Supralittoral amphipod abundance across habitats on Mediterranean temperate beaches. *Journal of Coastal Conservation*, 17, pp.841–849.

Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. *Ecological Society of America*, 78, pp.1146–1156.

Peacor, S., and E. E. Werner. 2004. How dependent are species-pair interaction strengths on other species in the food web? *Fisheries and Wildlife*, 85, pp.2754–2763.

Peacor, S. D., and E. E. Werner. 2008. Nonconsumptive effects of predators and trait-mediated indirect effects. *Chichester: eLS. John Wiley and Sons Ltd.* Published online 15 December 2008. http://www.els.net/WileyCDA/ElsArticle/refId-a0021216.html.

Perkins, E. J. 1974. *The biology of estuaries and coastal waters.*, London: Academic Press.

Persson, L-E. 1999. Growth and reproduction in two brackish water populations of *Orchestia gammarellus* (Amphipoda: Talitridae) in the Baltic Sea. *Journal of Crustacean Biology*, 19, pp.53–59.

Pettorelli, N., A. Hillborn, C. Duncan, and S. M. Durant. 2015. Individual variability: the missing component to our understanding of predator-prey interactions. *Advances in Ecological Research*, 52, pp.19-44.

Pienkowski, M. W. 1983. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behavior of their shorebird predators. *Marine Ecology Progress Series*, 11, pp.141–150.

Pinheiro, L., D. Bates, S. DebRoy, and D. Sardar. 2015. nlme: Linear and nonlinear mixed effects models. R package version 3.1-120, http://CRAN.R-project.org/package=nlme.

Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. *Limnology and Oceanography*, 4, pp.386–397.

Portenko, L. A. 1968. Wanderfalke "wassert" im meer. *Falke*, 15, p.174.

Posey, M. H., and A. H. Hines. 1991. Complex predator-prey interactions within an estaurine benthic community. *Ecology*, 72, pp.2155–2169.

Poulin, R., and W. J. Hamilton. 1995. Ecological determinants of body size and clutch size in amphipods: a comparative approach. *Functional Ecology*, 9, pp.364–370.

Pound, H. E. 1936. Notes on the flight of the sparrowhawk. *British Birds*, 30, pp.183–189.

Prater, A. J. 1981. *Estuary birds of Britain and Ireland*, Berwick upon Teed: T and A. D. Poser.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, 86, pp.501–509.

Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, 88, pp.2744–2751.

Pulliam, H. R. 1973. On the advantages of flocking. *Journal of Theoretical Biology*, 38, pp.419–422.

Pulliam, H. R. 1974. On the theory of optimal diets. *The American Naturalist*, 108(959), pp.59–74.

Puttick, G. M. 1984. Foraging and activity patterns in wintering shorebirds. In J. Burger and B. L. Olla eds, *Behavior of marine animals volume 6 - current perspectives in research: shorebirds. migration and and foraging behavior*. New York: Plenum Press.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov.1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology*, 52, pp.137–154.

Quinn, J. L., and W. Cresswell. 2004. Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology*, 73, pp.143–154.

Quinn, J. L., and W. Cresswell. 2005. Escape response delays in wintering redshan, *Tringa totanus*, flocks: perceptual limits and economic decisions. *Animal Behaviour*, 69, pp.1285–1292.

Quinn, J. L. and W. Cresswell. 2006. Testing domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. *Proceedings of the Royal Society London, Series B-Biological Sciences*, 273, pp.2521–2526.

Quinn, J. L., and W. Cresswell. 2012. Local prey vulnerability increases with multiple attacks by a predator. *Oikos*, 121, pp.1328–1334.

Rabosky, D., and A. McCune. 2010. Reinventing species selection with molecular phylogenies. *Proceedings of the Royal Society of London, Series B-Biological Sciences*, 25, pp.68-74.

Raposa, K. B., K. Wasson, E. Smith, J. A. Crooks, P. Delgado, S. H. Fernald, M. C. Ferner, A. Helms, L. A. Hice, J. W. Jordan, B. Puckett, D. Sanger, S. Shull, L. Spurrier, R. Stevens, and S. Lerberg. 2016. Assessing tidal marsh resilience to sea-level rise at broad geographic scales with multi-metric indices. *Biological Conservation*, 204 (Part B), pp.263–275.

Reading, C. J., and S. McGrorty. 1978. Seasonal variations in the burying depth of *Macoma balthica* (L.) and its accessibility to wading birds. *Estuarine and Coastal Marine Science*, 6, pp.135–144.

Rehfisch, M. M., S. J. Holloway, and G. E. Austin. 2003. Population estimates of waders on the non-estuarine coasts of the UK and Isle of Man during the winter of 1997-98. *Bird Study*, 50, pp.22–32.

Reid, D. M. 1947. Talitridae (Crustacea Amphipoda) synopsis of British fauna. *Journal of the Linnean Society of London*, 7, pp.1–25.

Rendhal, A. 2013. Cross Validated - REML vs ML stepAIC. Available at: http://stats.stackexchange.com/questions/41123/reml-vs-ml-stepaic [Accessed February 27, 2017].

Rinehart, S. A., S. C. Schroeter, and J. D. Long. 2017. Density-mediated indirect effects from active predators and narrow habitat domain prey. Ecology, in press.

Rippe, H., and V. Dierschke. 1997. Picking out plum jobs: feeding ecology of curlews *Numenius arquata* in a Balstic Sea wind flat. *Marine Ecology Progress Series*, 159, pp.239–247.

Ripple, W. J., and R. L. Beschta. 2008. Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park. *Biological Conservation*, 141, pp.1249-1256.

Roberts, E. L. 1946. Unusual behaviour of peregrine falcon. *British Birds*, 39, pp.318–319.

Roberts, G. 1995. A real-time response of vigilance behavior to changes in group-size. *Animal Behaviour*, 50, pp.1371–1374.

Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour*, 51, pp.1077–1086.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behaviour of forest birds. *The Auk*, 101, pp.672–684.

Rosenblatt, A. E., and O. J. Schmitz. 2016. Climate change, nutrition and bottom-up and top-down food web processes. *Trends in Ecology and Evolution*, 31, pp.965-975.

Rosenzweig, M. L. 1973. Evolution of the predator isocline. *Evolution*, 27, pp.84–94.

Rossano, C., S. Gambineri, L. Fanini, V. Durier, C. Rivault, and F. Scapini. 2009. Behavioural adaptations in talitrids from two Atlantic beaches. *Estuarine Coastal and Shelf Science*, 85, pp.573–584.

Rossano, C., and F. Scapini. 2009. Endogenous locomotor activity rythmn of two sympatric species of talitrids (Crustacea, Amphipoda) from a sandy beach of Tuscany, Italy A. Bayed, ed. *Sandy Beaches and Costal Zone Management - Proceedings of the Fifth International Symposium on Sandy Beaches*, pp.81–85.

Royama, T. 1971. Evolutionary significance of predators' response to local differences in prey density. A theoretical study. In P. J. den Boer and G. R. Gradwell, eds. *Dynamics of Populations*. Wageningen: Centre for Agricultural Publishing, pp. 344–357.

R Studio Team. 2015. R Studio integrated development for R. R Studio Inc (version 0.99.486 - 2015).

Sánchez, M. I., A. J. Green, and E. M. Castellanos. 2005. Seasonal variation in the diet of redshank *Tringa totanus* in the Odiel marshes, southwest Spain: a comparison of faecal and pellet analysis. *Bird Study*, 52, pp.210-216.

Sansom, A., J. Lind, and W. Cresswell. 2009. Individual behavior and survival: the roles of predator avoidance, foraging success, and vigilance. *Behavioral Ecology*, 20, pp.1168–1174.

Santos, C. D., S. Saraiva, J. M. Palmeirim, and J. P. Granadeiro. 2009. How do waders perceive buried prey with patchy distributions? The role of prey density and size of patch. *Journal of Experimental Marine Biology and Ecology*, 372, pp.43–48.

Sars, G. O. 1890. *An account of the crustacea of Norway. Vol 1. Amphipoda*, Christania: Cammermeyers.

Scapini, F., M. Fallaci, and M. C. Mezzetti. 1996. Orientation and migration in *Talitrus saltitor*. *Revista Chilena de Historia Natural*, 69, pp.553–563.

Schmitz, O. J. 1994. Resource edibility and trophic exploitation in an old-field food web. *Proceedings of the National Academy of Sciences, USA*, 91, pp.5364–5367.

Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *The American Naturalist*, 151, pp.327–342.

Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology*, 88, pp.2415–2426.

Schmitz, O. J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science*, 319, pp.953-954.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on fod web interactions. *Ecology*, 78, pp.1388–1399.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7, pp.153–163.

Schmitz, O. J., and K. B. Suttle. 2001. Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, 82, pp.2072–2081.

Schneider, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. *Ecology*, 65, pp.1820–1827.

Schoener, T.W. 1989. Food webs from small to the large. *Ecology*, 70, pp.1559–1589.

Schradin, C. 2000. Confusion effect in a reptilian and primate predator. *Ethology*, 106, pp.691–700.

Schrama, M. J. J., M. P. Berg, and H. Olff. 2012. Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession. *Ecology*, 93, pp.2353–2364.

Schrama, M. J. J., P. Heijing, and H. J. van Wijnen. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia*, 172, pp.231–243.

Shepard, E., C. Williamson, S. Windsor. 2016. Fine-scale flight startegies of gulls in urban airflows indicate risk and reward in city living. *Philosophical Transactions of the Royal Society, London, B Biology*. Published online 26 September 2016. http://dx.doi.org/10.1098/rstb.2015.0394

Sheriff, M. J., E. K. McMahon, C. K. Krebs, and R. Boonstra. 2015. Predator-induced maternal stress and population demography in snowshoe hares: the more severe the risk, the longer the generational effect. *Journal of Zoology*, 296, pp. 305-310.

Shiino, Y., and K. Kitazawa. 2012. Stealth effect of red shell in (*Laqueus rubellus*) (Brachiopoda, Terebratulida) on the sea bottom: an evolutionary insight into the predator-prey interaction. *International Scholarly Research Network Zoology*, 2012, pp.1-7.

Shimizu, A., I. Dohozono, M. Nakaji, D. A. Roff, D. G. Miller III, S. Osato, T. Yajima, S. Niitsu, N. Utsugi, T. Sugawara, and J. Yoshimura. 2014. Fine-tuned bee-flower coevolutionary state hidden within multiple pollination interactions, *Scientific Reports*, 4, pp.1-9.

Siddon, C. E., and J. D. Witman. 2004. Behavioral indirect interactions: multiple predator effects and prey switching in the rocky subtidal. *Ecology*, 85, pp.2938–2945.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science*, 210, pp.1041–1043.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta-Hoffmanni*. *Ecology*, 63, pp.786–796.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In W. C. Kerfoot and A. Sih, eds. *Predation: direct and indirect impacts on aquatic communities*. Hanover, New Hampshire, USA: University Press of New England, pp. 203–224.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Srohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, 16, pp.269–311.

Sih, A., G. Enlund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution*, 13, pp.350–355.

Sinclair, A. R. E., and P. Arcese. 1995. Population consequences of predation sensitive foraging - the Serengeti wildebeest. *Ecology*, 76, pp.882–891.

Sitters, H. P. 2000. *The role of night-feeding in shorebirds in an estuarine environment with specific reference to mussel-feeding oystercatchers*. PhD Thesis, University of Oxford.

Smith, P. C. 1975. *A study of the wintering feeding ecology and feeding behaviour of the bar-tailed godwit, Limosa lapponica*. Ph.D Thesis, University of Durham.

Soluk, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, 74, pp.219–225.

Soluk, D. A., and J. S. Richardson. 1997. The role of stoneflies in enhancing growth of trout: a test of the importance of predator-predator facilitation within a stream community. *Oikos*, 80, pp.214–219.

van Son, T. C., and M. Thiel. 2006. Multiple predator effects in an intertidal food web. *Journal of Animal Ecology*, 75, pp.25–32.

Spaethe, J., J. Tautz, and L. Chittka. 2001. Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proceedings of the National Academy of Sciences of the United States of America*, 98, pp.3898–3903.

Spicer, J. I., and U. Janas. 2006. The beachflea *Platorchestia platensis* (Krøyer, 1845): a new addition to the Polish fauna (with a key to Baltic talitrid amphipods). *Oceanologia*, 48, pp.287–295.

Spicer, J. I., P. G. Moore, and A. C. Taylor. 1987. The physiological ecology of land invasion by the Talitridae (Crustacea, Amphipoda). *Proceedings of the Royal Society Series B-Biological Sciences*, 232 (1266), pp.95–124.

Spiller, D. A., and T. W. Schoener. 1990. a terrestrial field experiment showing the impact of eliminating top predators on foliage damage. *Nature*, 347, pp.469–472.

Sprung, M., and M. Machado. 2000. Distinct life histories of peracarid crustaceans in a Rio Formosa salt marsh (S. Portugal). *Wetlands Ecology and Management*, 8, pp.105–115.

Staines, B. W. 1976. The use of natural shelter by red deer *Cervus elaphus* in relation to weather in North-east Scotland. *Journal of Zoology*, 180, pp.1–8.

Staines, B. W. 1977. Factors affecting the seasonal distribution of red deer *Cervus elaphus* at Glen Dye, North-east Scotland. *Annals of Applied Biology*, 87, pp.495–512.

Steele, D.H., and V. J. Steele. 1991. Morphological and environmental restraints on egg production in amphipods. In A. Wenner and A. Kuris, eds. *Crustacean issues vol 7. Crustacean egg production*. Rotterdam: AA Balkema, pp. 157–170.

Stevenson, J. 2002. *The benefits to fisheries of UK intertidal salt marsh areas. RandD Technical Report E2-061/TR*, Bristol.

Stiling, P. B., V. Brodbeck, and D. R. Strong. 1991. Population increases of planthoppers on fertilized salt-marsh cord grass may be prevented by grasshopper feeding. *Florida Entomology*, 74, pp.88–97.

Stillman, R. A., J. D. Goss-Custard, and M. J. Alexander. 2000. Predator search pattern and the strength of interference through prey depression. *Behavioral Ecology*, 11, pp.597–605.

Stirling-Aird, P. 1977. Peregrine apparently hunting on ground. *Scottish Birds*, 9, p.347.

Studd, M., R. Montgomerie, and R. J. Robertson. 2011. Group size and predator surveillance in foraging house sparrows (*Passer domesticus*). *Canadian Journal of Zoology*, 61, pp.226–231.

Sutherland, T. F., P. C. F. Sheperd, and R. W. Elner. 2000. Predation on meiofaunal and macrofaunal invertebrates by western sandpipers (*Calidris mauri*): evidence for dual foraging modes. *Marine Biology*, 137, pp.983–993.

Sutherland, W. J., and G. A. Parker. 1998. Interference with ideal-free models. *Trends in Ecology and Evolution*, 13, p.410.

Tellier, A., S. Moreno-Gáme, and W. Stephan. 2014. Speed of adaptation and genomic footprints of host-parasite coevolution under arms race and trench warfare dynamics. *Evolution*, 68, pp.2211-2224.

Terry, J. C. D., R. J. Morris, M. B. Bonsall. 2017. Trophic interaction modifications: an empirical and theoretical framework. *Ecology Letters*, in press.

Thirgood, S. J., and R. Hewson. 1987. Shelter characteristics of mountain hair resting sites. *Holarctic Ecology*, 10, pp.294–298.

Thomas, R., I. Vaughan, and J. Lello. 2015. *Data analysis with R statistical software*, Caerphilly: Eco-explore.

Toy, T. J., A. J. Kuhaida, and B. E. Munson. 1978. The prediction of mean monthly soil temperature from mean monthly air temperature. *Soil Science*, 129, pp.181–189.

Tremblay, A., and J. Ransijn. 2015. LMERConvenienceFunctions: Model selection and post-hoc analysis for (G)LMER Models. R package version 2.10.

Trussell, G. C., P. Ewanchuck, M. Bertness, and B. R. Silliman. 2004. Trophic cascades in rocky shore tide pools: distinguishing lethal and non-lethal effects. *Oecologia*, 139, pp.427–432.

Trussell, G. C., and O. J. Schmitz. 2012. Functional traits, trophic control and consequences of foraging. In T. Ohgushi, O. Schmitz, and R. D. Holt, eds. In *Trait-mediated interactions - ecological and evolutionary perspectives.* Cambridge: Cambridge University Press.

Tyler, J. A., and D. P. Clapp. 1995. Perceptual constraints on stream fish habitat selection: effects of food availability and water velocity. *Ecology of Freshwater Fish*, 4, pp.9–16.

Uetz, G. W., J. Boyle, C. S. Hieber, and R Stimson Wilcox. 2002. Antipredator benefits of group living in colonial web-building spiders: the "early warning" effect. *Animal Behaviour*, 63, pp.445–452.

Ugolini, A. 1989. Orientation in the water and antipredatory behaviour in sandhoppers. *Marine Freshwater Behaviour and Physiology,* 14, pp.223-230.

Underwood, R. 1982. Vigilance behaviour in grazing african antelopes. *Behaviour*, 79, pp.81–107.

Valone, T. J. and S. L. Lima. 1987. Carrying food items to cover for consumption: the behavior of ten bird species feeding under the risk of predation. *Oecologia*, 71, pp.286–294.

Vermeij, G. J. 1987. *Evolution and escalation: an ecological history of life*, New Jersey: Princetown University Press.

Vermeij, G. J. 2012. The limits of adaptation: humans and the predator-prey arms race. *Evolution*, 66, 2007-2014.

Vijayan, S., D. W. Morris, and B. E. McLaren. 2012. Prey habitat selection under shared predation: tradeoffs between risk and competition. *Oikos*, 121, pp.783-789.

Vince, S. W., I. Valiela, N. Backus, and J. M. Teal. 1976. Predation by the salt marsh killfish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. *Journal of Experimental Marine Biology and Ecology*, 23, pp.255–266.

Vine, I. 1973. Detection of prey flocks by predators. *Journal of Theoretical Biology*, 40, pp.207–210.

Voous, K. H. 1961. Records of peregrine falcons on the Atlantic ocean. *Ardea*, 49, pp.176–177.

Wada, Y., K. Iwasaki, and Y. Yusa. 2015. Prey density strengths of density and trait-mediated indirect interactions of predators on an algal community. *Journal of Experimental Marine Biology and Ecology*, 468, pp.67-73.

Walsberg, G. E. 1986. Thermal consequences of roostsite selection: the relative importance of three modes of heat conservation. *The Auk*, 103, pp.1–7.

Waterhouse, F. L. 1955. Micro climatological profiles in grass cover in relation to biological problems. *Quarterly Journal of the Royal Meteorological Society*, 81, pp.63–71.

Watkin, E. E. 1941. The yearly lifecycle of *Corophium volutator*. *Journal of the British Ecological Society*, 10, pp.77–93.

Watson, M., N. J. Aebischer, and W. Cresswell. 2007. Vigilance and fitness in grey partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecology*, 76, pp.211–221.

Weeks, J. M., and P. S. Rainbow. 1992. The effect of salinity on copper and zinc concentrations in three species of talitrid amphipods (Crustacaea). *Comparative Biochemistry and Physiology*, 101C, pp.399–405.

Werner, E. E. 1991. Non-lethal effects of a predator on competitive interactions between two anuran larvae. *Ecology*, 72, pp.1709–1720.

Werner, E. E. 1992. Individual behavior and higher-order species interactions. *The American Naturalist*, 140, Suppl, pp.S5–S32.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist*, 142, pp.242–272.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, 55, pp.1042–1052.

Werner, E.E., and G. G. Mittelbach. 1981. Optimal foraging: field tests of diet choice and habitat switching. *American Zoologist*, 21, pp.813–829.

Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. *Ecology*, 64, pp.1525–1539.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, pp.1083–1100.

West, D. L., and A. H. Williams. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina antiflor*a (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology*, 100, pp.75–95.

Westhoff, V. 1971. The dynamic structure of plant communities in relation to the objectives of conservation. In E. Duffey and A. S. Watt, eds. *The scientific management of plant communities for conservation*. Oxford: Blackwell Scientific Publications.

Whitfield, D. P. 1985. Raptor predation on wintering waders in southeast Scotland. *Ibis*, 127, pp.544–558.

Whitfield, D. P. 1988. Sparrowhawks *Accipiter nisus* affect the spacing behaviour of wintering turnstone *Arenaria interpres* and redshank *Tringa totanus*. *Ibis*, 130, pp.284–287.

Whitfield, D. P. 2003. Redshank *Tringa totanus* flocking behaviour, distance to cover and vulnerability to sparrowhawk *Accipiter nisus* attack. *Journal of Avian Biology*, 34, pp.163–169.

Whitington, P. M., and J. P. Bacon. 1997. The organization and development of the arthropod ventral nerve cord: insights into arthropod relationships. In R. A. Fortey and R. H. Thomas, eds. *Arthropod relationships*. London: Chapman and Hall, pp. 295–304.

Whittingham, M. J., and K. L. Evans. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis*, 146(Supp. 2), pp.210–220.

Whittingham, M. J., and H. M. Markland. 2002. The influence of substrate on the functional response of an avian granivore and its implications for farmland bird conservation. *Oecologia*, 130, pp.637–644.

Wiersma, P., and T. Piersma. 1994. Raptor predation on wintering waders in the annual cycle of red knots. *Condor*, 96, pp.257–279.

Wildish, D. J. 1969. *Studies on the taxonomy, ecology and behaviour of Orchestia gammarella (Pallas), O. mediterranea A. (Costa) and O. cavimana (Heller) in the Medway Estuary*. PhD Thesis, University of London.

Wildish, D. J. 1970a. Locomotive activity rythmns of some littoral *Orchestia* (Crustacea: Amphipoda). *Journal of the Marine Biological Association of the United Kingdom*, 50, pp.241–252.

Wildish, D. J. 1970b. Some factors affecting the distribution of *Orchestia leach* in estauries. *Journal of Experimental Marine Biology and Ecology*, 5, pp.276–284.

Wildish, D. J. 1972. Post embryonic growth and age in some littoral *Orchestia* (Amphipoda, Talitridae). *Crustaceana*, 3, pp.267–274.

Wildish, D. J. 1979. Reproductive consequences of the terrestrial habitat in *Orchestia* (Crustacea, Amphipoda). *International Journal of Invertebrate Reproduction*, 1, pp.9–20.

Wildish, D. J. 1987. Estuarine species of *Orchestia* (Crustacea, Amphipoda, Talitroidea) from Britain. *Journal of the Marine Biological Association of the United Kingdom*, 67, pp.571–583.

Wildish, D. J. 1988. Ecology and natural history of aquatic Talitroidea. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, 66, pp.2340–2359.

Willason, S. W. 1981. Factors influencing the distribution and coexistence of *Pachygrapsus crassipes* and *Hemigrapsus oregonensis* (Decapoda: Grapsidae) in a California salt marsh. *Marine Biology*, 64, pp.125 – 133.

Williams, J. A. 1980. Environmental influence on the locomotor activity rythmn of *Talitrus saltator* (Custacea: Amphipoda). *Marine Biology*, 57, pp.7–16.

Williamson, D. I. 1951. Studies in the biology of talitridae (Crustacea, Amphipoda): effects of atmospheric humidity. *Journal of the Marine Biological Association of the United Kingdom*, 30, pp.73–90.

Wilson, E. E., and E. M. Wolkovich. 2011. Scavenging: how carnivores and carion structure communities. *Trends in Ecology and Evolution*, 26, pp.129-135.

Witherby, H. F., F. C. R. Jourdain, N. F. Ticehurst, and B. W. Tucker. 1939. *The handbook of British birds 3*, London: H. F and G. Witherby.

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, 73, pp.3–36.

Woodward, B. D. 1982. Tadpole competition in a desert anuran community. *Oecologia (Berlin)*, 54, pp.96–100.

Woodward, B. D. 1983. Predator-prey interactions and breeding-pond use of temporary pond species in a desert anuran community. *Ecology*, 64, pp.1549–1555.

Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology*, 73, pp.981–991.

World Sea Temperature. 2017. Dunbar sea temperature. Available at: https://www.seatemperature.org/europe/united-kingdom/dunbar-february.htm [Accessed February 21, 2017].

Yasue, M., J. L. Quinn, and W. Cresswell. 2003. Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in redshanks. *Functional Ecology*, 17, pp.727–736.

Ydenberg, R. C., and L. M. Dill. 1986. The economies of fleeing from predators. *Abvances in the Study of Behaviour*, 16, pp.229–249.

Zaklan, S. D., and R. Ydenberg. 1997. The body size-burial depth relationship in the faunal clam *Mya arenaria*. *Journal of Experimental Marine Biology and Ecology*, 215, pp.1–17.

Zaman, L., J. R. Meyer, S. Devangam, D. M. Bryson, R. E. Lenski, and C. Ofria. 2014. Coevolution drives the emergence of complex traits and promotes evolvability. *PLOS Biology*. 12, pp.1-9.

Zeileis, A., and T. Hothorn. 2002. Diagnostic checking in regression relationships. *R News*, 2, pp.7–10.

Zou, K., G. Lacroix, and S. Barot. 2016. Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, Special Feature, pp.1–36.

Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. *Analysing Ecological Data*, New York: Springer-Verlag.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*, New York: Springer-Verlag.

Zwarts, L., and J. H. Wannik. 1993. How the food-supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body-weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, 31, pp.441–476.